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# THE CONDOR

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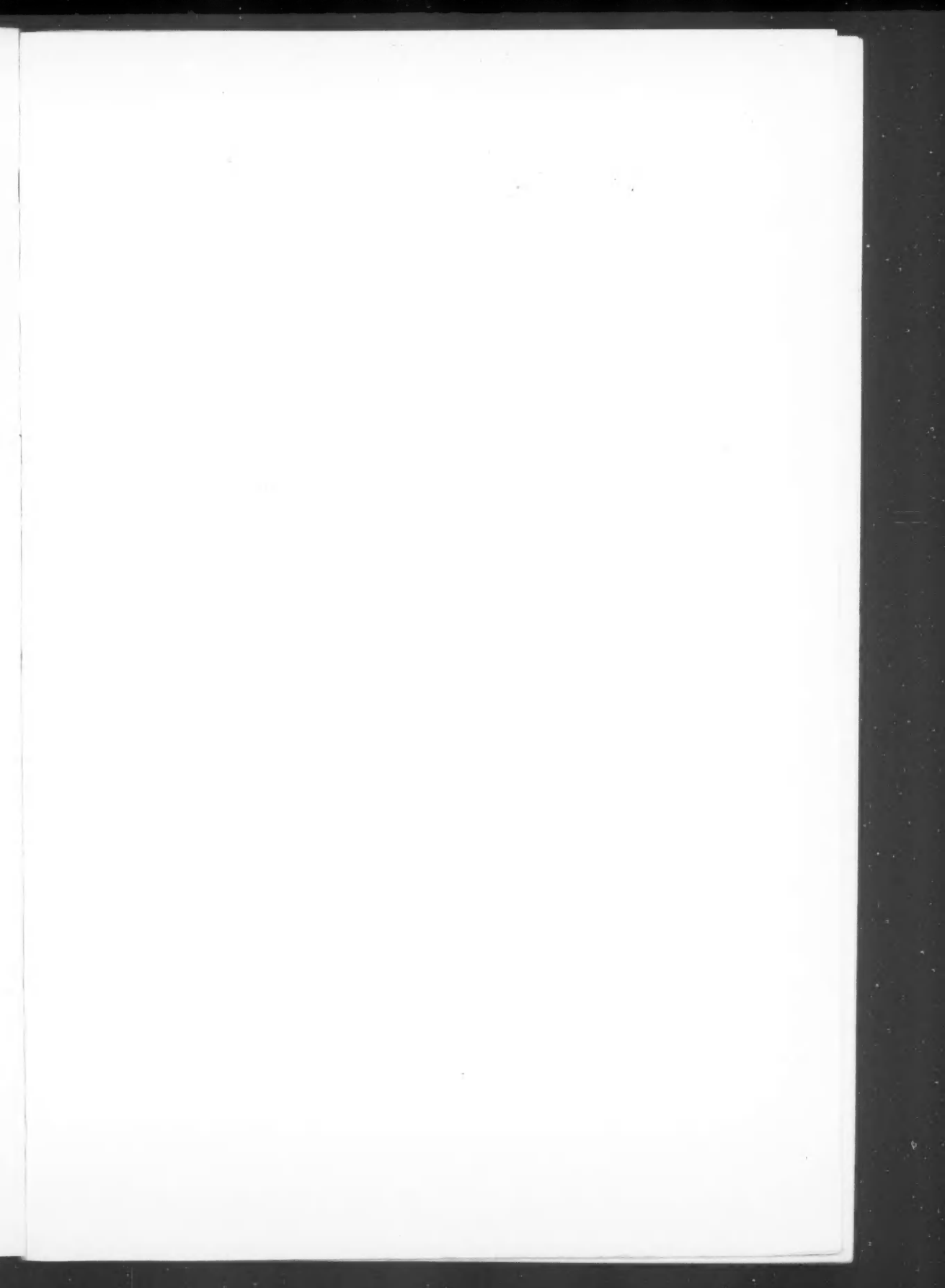
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BRAZILIAN MANAKINS

*HETEROCERCUS LINDEATUS*

"*PIPRA ANOMALA*," hybrid

*PIPRA AUREOLA AURANTIOCOLLIS*

Two-thirds natural size

From a painting by Don R. Eckelberry



# THE CONDOR

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## INTERGENERIC HYBRIDS IN THE FAMILY PIPRIDAE

By KENNETH C. PARKES

The Neotropical manakins of the family Pipridae include a number of strikingly sexually dimorphic species whose males gather at communal displaying areas, to which females come and at which copulation takes place without the formation of a lasting pair bond. Such a pattern of reproductive behavior is found in certain families of birds, notably the grouse and birds of paradise, in which hybridization is especially common. Sibley (1957) gave some attention to the family Pipridae in his paper on sexual dimorphism and hybridization, although he knew of only a single supposed hybrid in this family. The present paper will review briefly the manakins previously identified as probable hybrids and will offer evidence of intergeneric hybrid origin of additional unique manakin specimens.

The only hybrid manakin mentioned by Sibley was "*Chiromachaeris coronata*" Boucard, 1879. Hellmayr (1929:75), who had examined the unique type, had "little doubt that this supposed species is nothing but a hybrid between *Manacus manacus* (subsp.) and one of the yellow-headed varieties of *Pipra erythrocephala*." Comparison of males of the hypothesized parent species with Boucard's plate and Hellmayr's description suggests that "*Chiromachaeris coronata*" may well be such a hybrid, although the identification of the *Pipra* parent is perhaps less certain than that of the *Manacus manacus* parent. Sibley (1957:178) made the following statement concerning this hybrid: "It is of interest that the males in these two species, although differing in many plumage characters, both have areas of orange-yellow on the head. It is tempting to speculate that such similar characters may have been the basis for the 'mistake' in identification by the female which led to this instance of hybridization." But *Manacus manacus* has no "area of orange-yellow on the head," and Dr. Sibley has written me that this statement was based on his erroneous impression that *M. vitellinus*, a yellow species, was conspecific with *M. manacus*. The two species are sympatric in northern Colombia.

Another record of a supposed intergeneric hybrid in the Pipridae was called to my attention by Mr. Thomas E. Lovejoy III, of Yale University. Gyldenstolpe (1951: 241-242) published a description and photograph of a specimen from Redempção, Rio Purús, Brazil, which he identified tentatively as *Teleonema f. filicauda* x *Manacus manacus* subsp. Although, as Gyldenstolpe points out, no species of *Manacus* is presently known from the Purús basin, *M. manacus* is common on other tributaries of the Amazon and may yet be found on the Purús. Except for this apparent absence of one of the supposed parent species at the collecting locality, Gyldenstolpe presents a convincing case for the hybrid origin of his specimen. In fact, the shape of the rectrices of Gyldenstolpe's bird recalls, as he mentions, the lost unique type of "*Pipra heterocerca*" Sclater, 1860. The description of the latter specimen suggests to me that it may well have been a hybrid between *Teleonema filicauda* and a race of *Pipra aureola* or *P. fasciicauda*; either of the latter could have supplied certain of the color characters present in the hybrid and not in *Teleonema filicauda*. The genera *Pipra* and *Teleonema* appear to be closely related, the latter being characterized only by the peculiar filiform structure of the rectrices of both sexes.

Another "species" of manakin known only from a unique type is *Muscicapa luteoce-*

*phala* Lesson, which Hellmayr (1906:326) assigned to the genus *Heterocercus*. Although Hellmayr states that this specimen, of unknown geographic origin, is structurally typical of *Heterocercus*, his description of its color together with its uniqueness suggest that this specimen should be re-examined with the possibility of hybrid origin in mind.

Todd (1925:97) described as *Pipra anomala*, sp. nov., a single specimen collected at Santarem, Amazon River, Brazil, on May 1, 1919, by Samuel M. Klages. Todd called attention to the fact that certain of the bird's characters, notably the pattern of the sides of the head and the shortness of the outermost rectrices, were without counterpart elsewhere in the genus *Pipra*. Hellmayr (1929:15-16) mentioned also the large size and especially large bill (for a *Pipra*) of *anomala*. He suggested that "the type may not be quite mature," although Todd had said that it "at first sight looks as if it were a young bird, but upon closer examination seems to be fully adult." These conjectures about age were apparently based on the peculiar mixture of green and black on the bird's back, although this is not attributable to molt; the individual feathers are part green, part black. Hellmayr (1929) and Meise (1938:154) accepted *Pipra anomala* Todd as a valid species.

While going over the manakins in the Carnegie Museum recently in another connection, I had occasion to re-examine the still unique type of *Pipra anomala*. Certain of its characters reminded me of a species currently placed far from *Pipra*, and further study has convinced me that "*Pipra anomala*" Todd is actually a hybrid between *Pipra aureola aurantiicollis* and *Heterocercus linteatus*, both of which are found at Santarem. I am happy to say that Mr. Todd fully agrees with this identification, the evidence for which follows.

The genus *Heterocercus*, as conceived by Hellmayr (1929), contained four "species." One is the problematical *H. luteocephalus* (Lesson), mentioned previously. Best known is *H. linteatus* (Strickland), widely distributed in Brazil south of the Amazon. *Heterocercus flavivertex* is found north of the Amazon, in Brazil, southern Venezuela and eastern Colombia. Another form, *H. aurantiivertex*, may prove to be a western race of *flavivertex*; it is known only from one young and three adult males from Ecuador and a tentatively identified young male from Perú (Hellmayr, 1929:91; de Schauensee, 1953:35). Members of this genus are rather large for manakins, and they are characterized particularly by having strongly graduated tails, with the outermost rectrices much shortened and narrowed. The seventh primary is longest, with the eighth and sixth equal. In *Pipra* the tail is short and square, and the eighth and seventh primaries are equal. Rictal bristles are poorly developed in *Heterocercus* (not absent as indicated by Hellmayr, 1910:3, in key), and they are fairly well developed in *Pipra*.

TABLE 1  
MEASUREMENTS, TO NEAREST 0.5 MILLIMETER, OF ADULT MALE MANAKINS

Species	No.	Wing (flat)	Tail	Bill <sup>1</sup>
<i>Pipra aureola aurantiicollis</i>	10	60.5-64.5 (63.0)	25-29 (27.85)	6.5-7.5 (7.15)
" <i>Pipra anomala</i> " (type)		74	39	8
<i>Heterocercus linteatus</i>	10	87-91 (88.75)	50.5-54.5 (52.15)	8-9.5 (8.8)

<sup>1</sup>Measurements of bill are from anterior edge of nostril.

In these structural characters, the type specimen of "*Pipra anomala*" falls between *Pipra* and *Heterocercus*. As mentioned by Todd, the outermost rectrices of his specimen are decidedly shorter than the rest and are also narrowed; the rest of the tail is square,

like that of a *Pipra* but longer. The bill is intermediate in size and shape between those of *Pipra aureola* and *Heterocercus linteatus*. Rictal bristles are of about the same length as those of the *Pipra*, but are more slender. The seventh primary is longest, as in *Heterocercus*, but it is barely longer than the eighth, which exceeds the sixth as it does in *Pipra*.

Males of *Heterocercus linteatus* have a silky white throatpatch, with elongated erectile feathers at the corners, which are used in a frontal display (illustrated by Sick, 1959:274). In the type of "*anomala*," the throat is pale orange, but the corner feathers can be seen to be slightly elongated.

In color, "*Pipra anomala*" appears almost completely intermediate, as shown on the color plate (see frontispiece). In *H. linteatus* there is a relatively small orange crownpatch. In *P. aureola* the entire crown and anterior mantle are composed of feathers fading from brilliant scarlet at the tip through yellow to white at the base. In "*anomala*" the crown and nape (but not the mantle) are of an orange approximating that of the crownpatch of *linteatus*, but with the feathers fading to white at the base as in *aureola*. The back, wings and tail are a mixture of the olive green of *linteatus* and the black of *aureola*; there is no trace of the sharply defined white patch on inner webs of remiges typical of the latter species.

On the underparts, the throat, as mentioned, is midway between the silky white of *linteatus* and the orange-yellow of *aureola*. At first sight, the breast is a pale, "washed-out" version of that of *aureola*. The bases of the feathers, however, are white in *aureola*; in the presumed hybrid they are blackish as in *linteatus*. The horseshoe-shaped black breastband of *linteatus* is represented in "*anomala*" by narrow black patches at the positions of the "arms" of the horseshoe. The abdomen differs from that of either of the presumed parents in being yellowish white, washed with olive gray on the flanks (the latter somewhat as in *linteatus*). The under tail coverts of *aureola* are black, the feathers nearest the vent having pale yellow bases. In *linteatus* the under tail coverts are pale

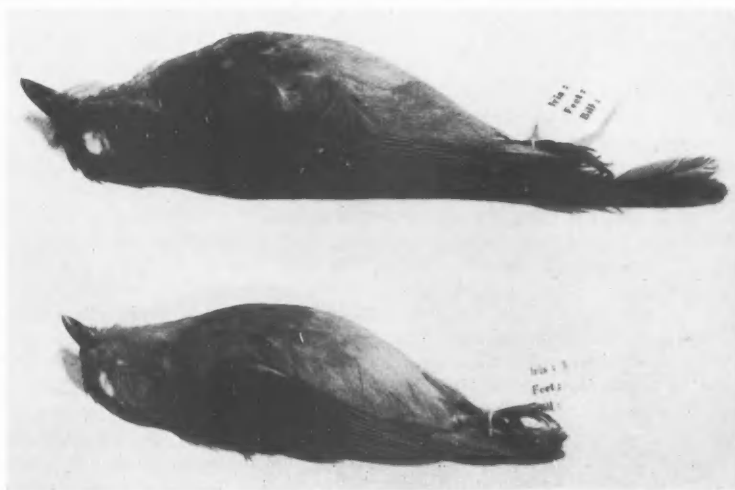


Fig. 1. Adult females of *Heterocercus linteatus* (upper) and *Pipra aureola aurantiicollis* (lower). Both figures are three-fourths natural size.

chestnut. In "*anomala*" these feathers are dark gray, with the bases white washed with pale orange.

One of the most interesting characters of "*anomala*" is the face pattern mentioned by Todd as being unique in the genus *Pipra*. Whereas in *Heterocercus linteatus* the entire head, except for the orange crownpatch and white throat, is black, in "*anomala*" only a facial "mask," somewhat interrupted at the lores, is black. There is no black at all on the head of *Pipra aureola*. In the northern species *Heterocercus flavivertex* (figured by Hellmayr, 1910: pl. 1, fig. 6) the greenish color of the back continues forward to the base of the bill, surrounding the bright crownpatch, with only a mask of blackish beginning just in front of the eye. This pattern in *H. flavivertex* suggests that the related *H. linteatus* carries the genetic potential for a similar mask, obscured by the development of black over the entire facial area. In the presumed hybrid, "*anomala*," the factor for the facial mask has been inherited and finds phenotypic expression.

In Sibley's discussion of *Manacus manacus* and *Pipra erythrocephala* as the presumed parents of "*Chiromachaeris coronata*," he mentioned the close similarity of their females. Although females of all sexually dimorphic manakins are rather plain, those of *Pipra aureola* and *Heterocercus linteatus* differ in size, proportions, and color as much as almost any two species in the family (see fig. 1). The similarity of the females is of less significance in analyzing hybridization in the Pipridae than in other families, as has been emphasized by Sick (1959:298), because of the courtship pattern in which females seek out males on their communal displaying grounds.

If, as the evidence seems to show, "*Pipra anomala*" is indeed a hybrid between *Heterocercus linteatus* and *Pipra aureola*, there can be little doubt that Hellmayr erred in placing *Heterocercus* at the end of the Pipridae and separating it from *Pipra* by such peculiar genera as *Massornis*, *Schifornis* and *Sapayoa*. As suggested by its general appearance and by the relative simplicity of its courtship patterns (Sick, 1959:274), *Heterocercus* is a less specialized manakin than is *Pipra*, and it should probably stand somewhat before *Pipra* in a linear sequence of genera. The reproductive behavior of *Heterocercus* differs sufficiently from that of *Pipra* that Dr. Sick, knowing both genera in life, was most reluctant to accept the idea of the hybrid origin of "*Pipra anomala*" until I sent him color slides of the pertinent skins.

Sibley (1957) has emphasized that genera in families of birds exhibiting great sexual dimorphism have all too often been based on male secondary sex characters which, having developed as reinforcements to reproductive isolation, may mask true close relationships. While this is undoubtedly true, I wonder whether the seeming overabundance of intergeneric as opposed to intrageneric hybrids may possibly be something other than an artifact based on oversplitting of genera. It occurs to me that selection favoring means of "preventing hybridization" would be most important among more closely related species. The less closely related two species are, the less chance there would appear to be for a reproductive "accident" resulting in hybridization. There would have been little selective pressure against such remote crossings simply because the situation would arise so infrequently. Behavioral and other isolating mechanisms would be developed to keep apart the closely related, essentially sympatric species which most frequently come into contact with one another during the reproductive season. Thus among the manakins we have no record of a hybrid between, say, two species of *Pipra*, but all reported hybrids appear to be intergeneric. This phenomenon may also appear in families in which a pair bond is formed, but in which a number of both closely and distantly related species may be sympatric. In the wood warblers, family Parulidae, a number of hybrids or presumed hybrids are known. Intergeneric hybrids include two

*Vermivora* x *Oporornis*, one *Parula* x *Setophaga*, and two *Parula* x *Dendroica* ("Sutton's Warbler," which may not be a hybrid but probably is). Except for these few intergeneric combinations, the only other wood warbler hybrids known to me are between what are rather obvious species-pairs, more closely related to one another than to any other species, which have probably evolved their divergences relatively recently. These include *Vermivora pinus* x *V. chrysoptera*, *Dendroica castanea* x *D. striata*, *Dendroica townsendi* x *D. occidentalis*, and especially *Dendroica coronata* x *D. auduboni*. The latter pair could probably best be considered as conspecific in view of the apparently unimpeded gene flow between the two forms. Another pair probably in this latter category consists of *Oporornis philadelphia* and *O. tolmiei*; these are so similar that hybrids are difficult to identify as such but equivocal specimens do exist.

Thus, among the Parulidae we have, at one extreme, hybrids between species-pairs some of which may not even be "good" species, and at the opposite extreme, intergeneric hybrids. Yet, particularly in the forests of northeastern North America, there are many species of sympatric congeneric parulids among which hybridization is not known to occur. This suggests that some particularly effective isolating mechanisms have developed among the North American wood warblers. These mechanisms rarely break down, but when they do, it is either among the closely related pairs, or between species so distantly related and so improbable as mates that no selection against such a crossing has developed. It is this latter situation that seems to have a parallel among the manakins, and it is of interest to note that Banks and Johnson (1961) independently came to virtually the same conclusion, based on their study of hybridization in North American hummingbirds.

Clearly this is a subject in which actual field observations in areas of sympatry would be highly illuminating, but the infrequency of "reproductive accidents" suggests that observers must be both persevering and fortunate to be able to contribute much toward our knowledge of how mixed matings come about or are prevented. Dr. David Snow, who has studied manakin behavior intensively in Trinidad, Panamá and British Guiana, has sent me the following notes, which he has kindly permitted me to quote: "I have seen, on two or three occasions only, ♀-plumaged (probably juvenile) *Manacus manacus* and *Pipra erythrocephala* associating together, with a certain amount of tentative display behaviour. On the one occasion when I knew the sex (by banding) of the *Manacus*, a definite juvenile ♂ *Manacus* was displaying quite persistently to a ♀-plumaged *Pipra*, which from its aggressive behaviour and incipient display movements was almost certainly a juvenile ♂; though the display of *Manacus* was typical of that which is normally directed to a ♀. Clearly one cannot make much out of such isolated observations, but they do suggest that there may at times be enough interaction between the two species for an occasional (abnormal?) individual to form a permanent attachment to the other species." Dr. Snow goes on to suggest that actual hybridization may come about if a young female has been closely associated with the "wrong" species as a juvenile. His observations of mating behavior together with certain structural differences suggest to him that, when *Manacus* and *Pipra* are involved, the latter is more probably the male.

Dr. Snow also raises the point that in the areas he has studied, manakins found together are nearly all of different genera. "Congeneric species are more often in different habitats ('avoiding' competition), so that a mating with a bird of another species is likely to be intergeneric simply because manakins of other genera are more likely to be at hand." This is undoubtedly true, and is one of the factors involved in the more efficient reproductive isolation between congeneric than between generically different

species. We must still determine the factors contributing to such reproductive isolation in areas in which congeneric species ARE found together.

#### ACKNOWLEDGMENTS

This paper was critically read in manuscript by W. E. Clyde Todd, David Snow, E. Thomas Gilliard, and Paul Slud. I am grateful for their comments and suggestions.

#### SUMMARY

Although the reproductive behavior of many species of Pipridae resembles that found in families characterized by relatively frequent hybridization, only two hybrid manakins have hitherto been reported: *Chiromachaeris coronata* Boucard = *Manacus manacus* x (probably) *Pipra erythrocephala*, and *Teleonema filicauda* x (probably) *Manacus manacus*. It is suggested that *Pipra heterocerca* Sclater may = *Teleonema filicauda* x *Pipra aureola* or *P. fasciicauda*, and that *Heterocercus luteocephalus* (Lesson) may be of hybrid origin. Evidence is presented to support the theory that *Pipra anomala* Todd = *Pipra aureola* x *Heterocercus linteatus*. It is suggested that selection against hybridization has developed most strongly among closely related species of birds, partly through geographical and ecological isolation, but allowing occasional intergeneric hybridization between unlikely combinations of parents.

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## REPRODUCTIVE CYCLE OF THE MALLARD DUCK

BY OSCAR W. JOHNSON

Considerable work has been done on the behavioral patterns associated with the reproductive cycle of waterfowl. The books by Sowls (1955) and Hochbaum (1959), and the papers by Ramsey (1956) and Johnsgard (1960) are notable in this regard. There has been, however, very little research on the gonadal changes associated with the cycle. With this in mind, a study was undertaken in southeastern Washington the main objective of which was to trace the cyclic changes of the reproductive organs of the Mallard (*Anas platyrhynchos*).

## METHODS

Wild Mallards (81 males and 57 females) were collected from March, 1958, through June, 1959. Five additional males were taken in May of 1960. An effort was made to record the undisturbed behavioral actions of each specimen immediately prior to collection. Such notes helped greatly in later categorization. The desired tissues were excised in the field and fixed in AFA solution (glacial acetic acid, 10 parts; 37 per cent formalin, 10 parts; 95 per cent alcohol, 30 parts; and distilled water, 50 parts). All collected materials were brought back to the laboratory for examination and the recording of various data. The laboratory procedures were as follows:

*Males*.—Testicular length and width (measured in the dorso-ventral plane) in millimeters were obtained with a vernier caliper. The testes used for microscopic analyses were dehydrated in dioxane and embedded in paraffin. The preparations were stained with Heidenhain's hematoxylin and counterstained lightly in eosin.

The penis was removed by cutting along its lines of attachment flush with the cloacal wall. This procedure was simplified by pressure eversion of the penis through the cloacal opening at the time of collection. After removal the penis was weighed. It was found that penis weight was a much better relative measurement than length.

*Females*.—The largest follicle on each ovary was measured in millimeters using the vernier caliper. Measurements were made in the same plane as the stigma. Oviduct length (to the nearest five millimeters) was measured by cutting the supporting ligaments (which tend to keep the structure in a convoluted position), and then gently straightening the tube along a millimeter rule.

*Both sexes*.—Bursae were dissected away from the cloacae, and their maximum outside length measured with a millimeter rule. Diameter measurements were made with a vernier caliper near the middle of each bursa. All excised structures, after having been carefully dissected away from extraneous tissues, were weighed to .001 gm. on a chain balance. Weighings were made in a sealed jar containing a piece of filter paper saturated with alcohol. This method minimized the degree of error from evaporation. The weight of the jar was standardized after every other weighing to maintain a high degree of accuracy. The feather development of each specimen was closely inspected. Plumage data were valuable in categorizing birds during later analyses.

## BURSA OF FABRICIUS

In juvenal Mallards, the bursa is a conspicuous, glandular organ with a well developed lumen. On the basis of bursae which were examined from flightless young, it appears that the size of the structure in Mallards is maximum at about the time flight is achieved. The mean bursal measurements for nine juveniles (males and females capable of flight) taken during July and August are as follows: length, 32.1 mm.; diameter, 8.0 mm.; and weight, 1.54 gm.



Much reduced remnant bursae were found in birds collected during the winter and spring of 1959. The retention of these remnant structures was not realized early in this study, and undoubtedly some remnant bursae were overlooked during the spring and summer of 1958. These reduced structures appear as slender, flattened pieces of tissue, and have no apparent lumen. Their occurrence poses an important question. Are remnant bursae strictly characteristic of yearling birds, or may such structures be retained indefinitely? It is possible that careful dissection would disclose the general retention of remnant bursae in adult Mallards. It is obvious that knowledge of the later regressive stages in bursae of Mallards and other waterfowl is inadequate. Work under controlled conditions is needed to clarify these details.

After the bursae of Mallards regress to a weight level of about 0.10 gm., they appear to persist with little change for an indefinite period. The mean measurements of 25 remnant bursae taken from late January through May are: length, 16.8 mm.; diameter, 2.0 mm.; and weight, 0.07 gm.

Among males, remnant bursae reached a very inconspicuous size by January 31, 1959. Hence in analyses, males taken after this date were considered adults. In females, birds of yearling status seemed obvious until February 22. Females containing very reduced bursae collected after the latter date were considered as adults.

#### MALE REPRODUCTIVE SYSTEM

##### TESTES

##### SPERMATOGENESIS

The following classification was developed to express the relative histological development in the testes of male Mallards taken throughout the annual cycle. Essentially these stages are a modification of those given by Johnston (1956).

*Stage 1.*—(Inactive condition—tubular lumina contain spermatogonia and a few primary spermatocytes; fig. 1a). Each tubule shows a peripheral row of spermatogonia. Most tubules also contain primary spermatocytes, which vary from merely a few individuals to one irregular row in some tubules. Primary spermatocytes may be wedged in toward the basal spermatogonia or lie toward the lumen well within the peripheral spermatogonia. A very few primary spermatocytes in synapsis are occasionally found. Most tubules show a small central lumen, which is generally bordered by considerable amounts of clear cytoplasmic material. Toward the end of this stage, primary spermatocytes tend to become more abundant and move closer to the lumen, and the cytoplasmic border becomes less apparent.

*Stage 2.*—(Increase in the number of primary spermatocytes, many of which are in synapsis, fig. 1b). An increase in both spermatogonia and primary spermatocytes is apparent. During early phases of Stage 2 (the initiation of recrudescence) primary spermatocytes in synapsis are found in scattered clumps throughout the section. During later phases, from one-fourth to one-half of all primary spermatocytes in a given field are in synapsis. Some tubules possess a lumen, but most tubules are filled with cells and the lumina as well as their clear cytoplasmic borders are obliterated.

*Stage 3.*—(Majority of primary spermatocytes in synapsis, and a few secondary spermatocytes present). Most tubules show one or two rows of spermatogonia and two or three rows of primary spermatocytes. Only a very few of the latter are not in synapsis. Some tubules show a few secondary spermatocytes. A few tubules possess a small lumen—most appear completely filled by the rapidly developing cells.

*Stage 4.*—(Secondary spermatocytes, some spermatids and immature spermatozoa, fig. 1c). Tubules generally show two rows of spermatogonia, with two or three rows of primary spermatocytes in synapsis. The central portions of most tubules have irregularly placed secondary spermatocytes and spermatids undergoing spermiogenesis. Few to moderate numbers of maturing spermatozoa can be found in many of the central areas of the tubules. All spermatozoa are immature and only a very few are attaching to Sertoli cells. There are no distinct open lumina—the tubules are filled with developing cells.



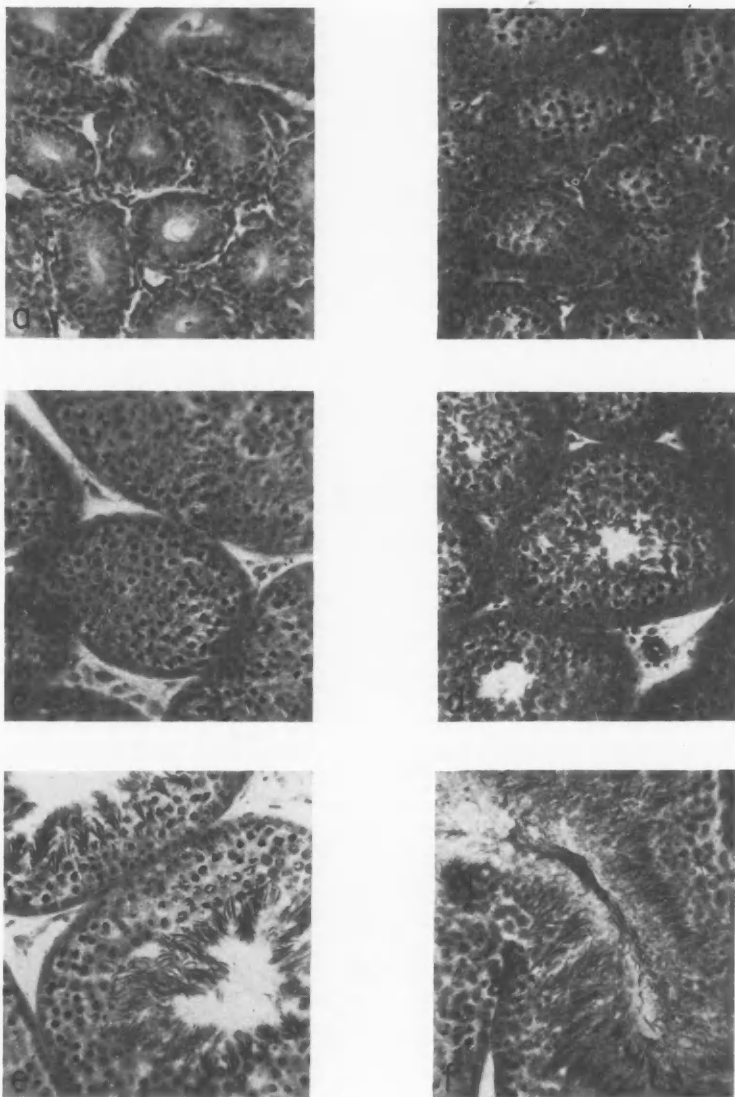


Fig. 1. Photomicrographs of testes of Mallards (*Anas platyrhynchos*) showing representative histologic stages. a, Stage 1; b, Stage 2; c, Stage 4; d, Stage 5; e, Stage 6; f, Stage 7. All photographs are approximately 240 $\times$ .

*Stage 5.*—(Large numbers of spermatids, and moderate numbers of spermatozoa, fig. 1d). Many spermatids showing various degrees of the spermiogenetic process are present. Many maturing spermatozoa are leaving central tubule areas and moving peripherally for attachment to Sertoli cells. Open tubular lumina, although small, are now becoming quite common. Some tubules contain well developed bundles of sperm attached to Sertoli cells. The first mature spermatozoa are apparently produced during this stage.

*Stage 6.*—(Full breeding condition, fig. 1e). Testes in this stage show maximum size, weight, and tubule diameter. Large numbers of maturing spermatozoa are grouped in regular bundles attached to Sertoli cells distributed around the course of each tubule. A few spermatozoa are present in the lumina of the tubules and probably represent mature sperm in the process of transit through the tubules to the duct system. Almost all tubules show a large central lumen.

*Stage 7.*—(Regression, fig. 1f). The first indication of regression is the casting off of large numbers of spermatozoa into the tubular lumina. From this point on, the other epithelial contents of the tubules are sloughed in order, and the tubules are filled with detritus and degenerating cells. During late periods of this stage, tubules contain small numbers of primary and secondary spermatocytes along with cellular detritus.

TABLE 1  
SUMMARY OF REPRODUCTIVE DATA FROM 86 MALE MALLARDS

Number of specimens	Range in testis weight (av. of right and left) in gms.	Distribution of spermatogenic stages	Range in penis weight in grams	Collection period
20	.075-4.940	Pre-breeding males—Paired but not yet sexually mature 1(1), 2(8), 3(4), 4(5), 5(2)	.289-2.946	2/21 to 4/6/58 11/24/58 to 4/4/59
11	3.270-15.844	Mature breeding males—Paired and sexually mature 6(11)	1.295-3.602	3/22 to 5/11/58 3/21 to 4/26/59
6	4.491-15.994	Early desertion drakes—Show no evidence of postnuptial molt 6(6)	1.740-2.780	4/12 to 4/27/58 4/12 to 4/26/59 and May, 1960
11	.086-8.632	Drakes undergoing postnuptial (eclipse) molt 6(3), 7(8)	.422-2.480	5/11 to 7/12/58 and May, 1960
8	.076-.211	Drakes undergoing prenuptial molt 1(4), 7(4)	.415-1.273	8/3 to 10/16/58
10	.077-.439	Adult drakes (winter)—Full plumage, not paired 1(4), 2(5) 3(1)	.310-1.307	11/13/58 to 3/15/59
4	.023-.043	Immature drakes (summer)—All in early prenuptial molt 1(4)	.010-.021	7/26 to 8/17/58
2	.048-.068	Immature drakes (fall)—Prenuptial molt well advanced 1(2)	.026-.039	9/28 to 10/24/58
14	.040-.127	Immature drakes (winter)—Prenuptial molt complete, not paired 1(6), 2(8)	.010-.876	11/23/58 to 1/31/59

Table 1 summarizes reproductive data for males. We may first note the distribution of the histologic stages of spermatogenesis with regard to the various categories into which the birds have been grouped.

Stage 6 (full maturity) is representative of paired breeding males. It is also found

in males which have recently deserted breeding territories and are in a transitional period between breeding and the postnuptial molt. In some birds, full maturity of the gonads tends to persist into the early stages of the postnuptial molt.

Regression (Stage 7) is a rather lengthy process which begins early in the period of postnuptial molt and persists in most birds well into the prenuptial molt period *during the fall* when the breeding plumage is again assumed.

Complete regression to Stage 1 occurs during the prenuptial (second fall) molt period. All testes appear to be fully regressed by the time that complete new prenuptial plumage is acquired. Stage 1 persists through most of the wintering period, and much courtship and pair formation is completed during this time of gonadal quiescence. Observations of wintering Mallards along the Snake River near Clarkston, Washington, disclosed sexual display and pair formation from early October onward. By late December and early January (the time of general male recrudescence) approximately 35 to 40 per cent of the males present were already paired.

The transitory stages (2, 3, 4, and 5) between inactive condition and complete recrudescence occur from midwinter through early spring. During these spermatogenic stages, males are generally mated and in a pre-breeding status.

#### WEIGHT AND SIZE RELATIONSHIPS

This analysis of testicular weight is based upon the mean weight of both testes in each specimen. The general practice in avian studies has been to use figures from just the left testis or from the larger of the two testes. It would seem that the mean weight more accurately denotes the reproductive condition of a given individual.

Table 2 gives a summary of testis weight and size relative to spermatogenic stages 1 through 6. Stage 7 is not included since it seems relatively meaningless to present calculations for the period of regression. The table is based upon adult birds and possible yearling birds which were taken after January 31, 1959 (see section on the bursa of Fabricius).

TABLE 2  
WEIGHT OF TESTES AND PENISES AND SIZE MEASUREMENTS OF TESTES RELATIVE TO  
SPERMATOGENIC STAGES

	Stage number					
	1 (9) <sup>1</sup>	2 (13)	3 (5)	4 (5)	5 (2)	6 (20)
Testis weight (gm.)						
Mean	0.109	0.154	0.520	1.967	3.970	8.234
Maximum	0.148	0.390	1.010	3.707	4.940	15.994
Minimum	0.077	0.075	0.218	0.975	3.000	3.270
Testis size (mm.)						
Mean length	10.44	11.57	17.29	25.84	33.02	41.48
Mean width	3.83	4.43	7.07	10.94	14.02	17.59
Max. length	11.70	15.15	22.85	31.70	33.80	51.70
Min. length	8.95	9.95	13.05	17.80	32.25	31.10
Max. width	4.45	6.37	8.90	15.35	15.00	23.45
Min. width	3.40	3.20	5.45	8.60	13.05	14.15
Penis weight (gm.)						
Mean	0.728	0.825	1.491	1.969	2.183	2.326
Maximum	1.273	1.598	1.911	2.946	2.840	3.602
Minimum	0.428	0.289	0.977	1.448	1.527	1.295

<sup>1</sup> Number of specimens available in each stage.

The general pattern of cyclic change in testis weight and size is evidenced by the means in the table. It is obvious that considerable overlap occurs between maximum and minimum figures. This overlap makes it impractical to attempt to ascertain the histologic condition of testes of Mallards on the basis of weight or size.

If the maximum and minimum weights in Stage 6 are considered relative to the mean value of Stage 1, a range of weight increase from about 30 to 146 times is indicated. One explanation for this range of individual variation might be the length of time that a particular male remains mated and territorial. A lengthy period of territoriality may allow continuing gonadal hypertrophy. The territorial period undoubtedly varies since nest destruction or desertion may cause the hen to start more than one nest. Another influencing factor may be the age of the bird. The lack of suitable techniques to determine accurately the age of waterfowl, and incomplete knowledge of the later regressive changes of the bursa, make it impossible to analyze this matter. It is noteworthy that a bursal remnant was found in a specimen with extremely large testes (mean weight, 15.8 gm.). Johnston (1956) showed definite testicular size differences in various age classes of California Gulls (*Larus californicus*). Wright and Wright (1944) demonstrated that the testes of year-old Redwinged Blackbirds (*Agelaius phoeniceus*) reached only two-thirds the size of adult organs. The need for work under controlled conditions with the waterfowl group is obvious. Höhn (1947) presents data which also indicate considerable weight variation in testes of Mallards of comparable histologic development.

Aside from the possible effects of the total period of sexual stimulation on males in Stage 6, it would also appear that the range in values throughout the spermatogenic cycle is greatly influenced by the present method of assigning rather broad stages to the spermatogenic process. Perhaps a more quantitative technique in arriving at histological considerations would lessen much of this variation.

It is informative to compare the gonad weights of regressed adults with those of immature birds. During the late summer, fall, and winter (August through December) the mean gonad weight for 16 regressed adults was 0.12 gm. During the corresponding period, the mean for 14 immature birds was 0.06 gm. There were no instances of overlap between maximum immature weights and minimum mature weights. By January, however, it appears that at least some yearling males contain gonads of a size comparable to that of adults. In a small sample of two adults and three immatures taken in January, one immature bird overlapped broadly with the adult values.

The weight difference found between the testes of adult and immature Mallards is similar to findings in other birds. Blanchard (1941) and Blanchard and Erickson (1949) report the same tendency in the testes of White-crowned Sparrows (*Zonotrichia leucophrys*). Kirschbaum and Ringoen (1936) found adult House Sparrows (*Passer domesticus*) to have larger testes than juveniles during the fall period. Wright and Wright (1944) found testes of adult Redwinged Blackbirds to be larger than testes of immature individuals throughout the quiescent period.

In most species of birds, the left testis is larger than the right. Mallards appear to deviate considerably from this general rule. Of 82 males in which the weights of both testes were obtained, there were 32 (39 per cent) in which the left testis was larger; 49 (59.7 per cent) in which the right testis was larger; and one (1.3 per cent) in which both testes were equal in weight.

#### RECRUDESCENCE

A great deal of variability in the maturity of testes was encountered during the recrudescence period in the late winter and spring. Such a phenomenon is probably to be

expected in a far-ranging migratory species like the Mallard. Birds collected in south-eastern Washington may be representative of different wintering conditions along the flyway (varied light intensities, and so on), and as a result show varied levels of sexual development.

It is also possible that the variation is to some degree induced by racial affinities. Wolfson (1942) showed a differential pattern of recrudescence development in juncos (*Junco oreganus*). He notes that migrant races are later in recrudescence, and that they tend to maintain the intermediate histologic stages of spermatogenesis for longer periods than nonmigratory juncos. Mallards that winter in this area may represent a fairly sedentary population, and hence might undergo recrudescence faster than birds destined to migrate for long distances before breeding.

Another factor which may cause variability in recrudescence is the possible influence of relative age. Wright and Wright (1944) found immature male Redwinged Blackbirds to be about three weeks behind the recrudescence of mature birds. Blanchard and Erickson (1949) found a tendency for the testes of immature White-crowned Sparrows to be of smaller size than those of adults, but there was no apparent difference as to the time of attainment of the various histologic stages of spermatogenesis. As previously discussed, the testes of immature Mallards are smaller than regressed mature testes. The differences, which appear to become much reduced by January, do not seem great enough to add much to the variability in recrudescence development. Also, as table 1 shows, recrudescence appears to begin at about the same time among both mature and immature birds.

The earliest indications of recrudescence (Stage 2 testes) were found in two males (one adult, one immature) both taken on December 11, 1958. General recrudescence among both immature and mature males appears to be underway by late December to early January in this region. If we assume that birds destined to nest in this area (the sedentary population) begin to recrudescence during this time, then a period of about three months is involved before full maturity is achieved in mid- to late March. Males beginning to regress (Stage 7) were found by mid-May, with increasing numbers present during early June. It thus appears that an individual drake may possess full sexual capacity for about 1.5 to 2.5 months.

#### REGRESSION

The postnuptial or eclipse molt furnishes a time scale with which one can approximate the rate of testicular regression. The important characteristics of the molt according to Hochbaum (1959) are as follows: the assumption of postnuptial plumage requires two or three weeks, during which time the molt is confined to the body feathers; when full postnuptial body plumage is acquired, a simultaneous molt of all remiges and rectrices occurs, rendering the bird flightless; the growth of new remiges and rectrices requires about 2.5 to 4 weeks, during which time the eclipse plumage is retained; when the growth of new flight feathers is completed, the prenuptial molt begins. A number of males in various stages of postnuptial and early prenuptial molt were collected. The data from these birds are summarized in table 3.

The beginning of regression appears somewhat variable in individual Mallards. In general, the first histologic indications of regression correspond with the early phases of the postnuptial molt during which one finds short, newly emerged eclipse feathers well hidden beneath the prenuptial plumage. There is an undetermined length of time following desertion of the territory during which sexual vigor is maintained. This, plus the fact that some birds retain full sexual capacity in the early stages of the postnuptial molt, may

have important implications in reneating behavior. Höhn (1947) also shows individual variability as to the start of regression during the early eclipse period. Seligmann and Shattock (1914) mention drake Mallards which in late spring and early summer still possessed full winter plumage while their testes were considerably regressed. Nothing of this sort was found in the present study, and it may be that the semi-domestication of the Mallards which these investigators were using introduced this variation.

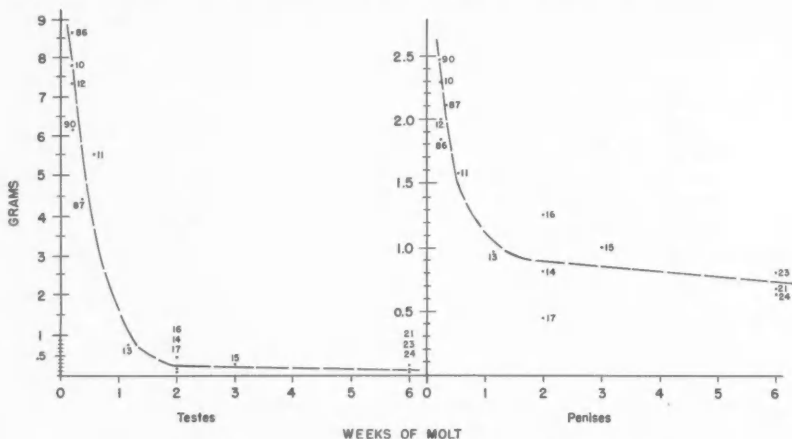


Fig. 2. Approximate weight regression of testes and penises of Mallards. Numerals refer to specimen numbers.

The data from table 3 can be plotted graphically as shown in figure 2. It appears from the graph that the regression of the testes of Mallards is a two-stage process. The first regressive change is fairly rapid. In the first 1.5 to 2.5 weeks of the postnuptial molt, the major part of regression is completed. Following this rapid initial regression, testis weights decrease very gradually into the time of prenuptial molt. This second phase appears to last for one to two months. The considerable time involved in testis regression of Mallards is also indicated by Höhn (1947) who collected males in almost complete prenuptial plumage which still showed histological indications of regression.

#### PENIS

The penis was found to undergo a cyclic change in weight paralleling the testicular cycle (table 2). Penis regression is similar to the two-stage process described for testicular regression. Data are summarized in table 3 and in figure 2.

The size of the juvenal penis remains almost constant for the first several months of the bird's life. Hochbaum (1942) states that the immature penis may remain little changed for from five to ten months. He notes that a few young Mallard drakes may assume the adult penis by mid-November, but that the majority do not reach this point until after the end of December. The first enlarging juvenal penises which I observed were found in late December. Considerable variation was found in penis weight after the first few enlarging organs were noted. Some birds appear to retain juvenalized penises into January, and perhaps even later. These variations probably reflect the span of the previous year's hatching season and the consequent relative age of the birds.

TABLE 3

COMPARATIVE ASPECTS OF REGRESSING TESTES AND PENISES IN BIRDS UNDERGOING THE POSTNUPTIAL AND EARLY PRENUPTIAL MOLTS

	Specimen number	Mean testis weight (gm.)	Spermatogenic stage	Penis weight (gm.)
Early stages of eclipse, postnuptial feathers 5 to 20 mm. long and completely hidden beneath prenuptial plumage	10	7.740	6	2.294
	11	5.511	7	1.575
	12	7.370	6	1.994
	86	8.632	7	1.820
	87	4.406	7	2.100
	90 <sup>1</sup>	6.140	6	2.482
Prenuptial plumage mottled with eclipse feathers	13	0.766	7	0.979
Complete postnuptial plumage, wing and tail feathers not yet cast	14	0.179	7	0.808
	16	0.508	7	1.246
	17	0.086	7	0.422
Complete postnuptial plumage, wing and tail feathers cast, growing stubs very short	15	0.248	7	0.999
Plumage dominantly of eclipse feathers, wing and tail feathers completely replaced, prenuptial molt just beginning	21	0.211	7	0.673
	23	0.108	1	0.797
	24	0.090	7	0.623

<sup>1</sup> Right testis damaged, weight applies to left testis only.

The penis of breeding birds is a very prominent, tapering, spiralled (corkscrew-like) structure. The surface is coarsely ridged with flaps of tissue which originate at each side of an external groove and extend transversely around the circumference of the organ. In many adult penises, the transverse ridges are tinged slightly with gray. Except for this variation, the penis is predominantly white. The morphological appearance of the penis changes markedly during regression and recrudescence. The regressed penis is only one-third to one-half the length of the mature organ and is much reduced in diameter. The transverse ridges become much lower, and the whole organ assumes a smooth, white, very slender appearance.

## FEMALE REPRODUCTIVE SYSTEM

*Cyclic weight and morphological changes.*—Table 4 summarizes data for females categorized on the basis of various stages in the annual cycle. Average figures show about a 100 to 1 relationship between the weight of recrudescing and regressed ovaries. When the variation among mature ovaries is considered, a range of about 85–120 to 1 is indicated. The period of time during which a female remains sexually stimulated appears to be an important variable factor. The maximum mature weight shown in table 4 represents the ovary of a bird which had ovulated at least 11 times. The minimum mature weight represents a bird which had ovulated but once. Relative age may have some possible influence on the degree of hypertrophy.

The immature ovary is a flat, inconspicuous organ which is commonly around 15 mm. in length, 5 mm. in width, and 1 to 2 mm. thick. The mean weight of five immature ovaries taken during summer was 0.083 gm. The surface is fissured with fine convolutions and shows no evidence of follicle enlargement. Gradual growth of follicles begins sometime during early fall. By late November the ovaries of most immature hens con-

TABLE 4  
WEIGHTS OF OVARIES AND OVIDUCTS AND MEASUREMENTS OF FOLLICLES AND OVIDUCTS  
FROM ADULT FEMALE MALLARDS AT VARIOUS LEVELS OF SEXUAL DEVELOPMENT<sup>1</sup>

Ovary weight (gm.) and follicle meas- urements (mm.)	Mature (2) <sup>2</sup>	Gravid (5)	Intermediate (10)	Early (2)	Wintering (6)
Mean	21.888	11.392	2.235	0.682	0.213
Maximum	25.687	14.572	4.626	0.897	0.281
Minimum	18.090	8.257	0.696	0.468	0.146
Largest follicles (range in mm.)	20 to 30	21.6 to 26.5	6.2 to 17.3	5 to 6	1.5 to 3.2
Oviduct weight (gm.)					
Mean	39.075 <sup>3</sup>	19.468	6.131	1.448	0.743
Maximum	62.560	26.525	13.828	1.914	0.993
Minimum	21.350	15.402	2.557	0.983	0.459
Oviduct length (mm.)					
Mean	342 <sup>3</sup>	259	148	95	90
Maximum	420	300	190	105	110
Minimum	245	210	100	85	85

<sup>1</sup> Mature—laying hens; Gravid—not yet laying, but nearing maturity on the basis of large follicles; Intermediate—weight relatively low, follicles 6.2 to 17.3 mm. in diameter; Early—only slight weight increase from the winter level, follicles 5 to 6 mm. in diameter; Wintering—quiescent organs low in weight, follicles 1.5 to 3.2 mm. in diameter.

<sup>2</sup> Number of specimens available in each category.

<sup>3</sup> Mature oviduct figures are based on three oviducts.

tain follicles of approximately the same size as those of regressed mature birds. After follicle enlargement begins there are no apparent macroscopic differences between mature and immature ovaries. With follicle enlargement the mean weight of immature ovaries increases considerably from summer levels. Nine such organs taken from late November to late February showed a mean of 0.202 gm. This figure is similar to the mean ovary weight for wintering adults (0.213 gm.) as given in table 4.

The oviduct of both gravid and laying hens is a long, highly convoluted, muscular structure. The regressed oviduct becomes flat and ribbon-like, with the exception of the vaginal area which retains a thicker, more muscular appearance. On the basis of the mature and wintering categories in table 4, the fluctuation in oviduct length appears to be about four to one.

Cyclic weight changes of the oviduct indicate about a 52 to 1 relationship between mature and regressed weight levels, with variations ranging from 28–84 to 1 (table 4). This range is likely dependent upon the same factors which influence the range in weight of the ovary. Individual oviduct weights were correlated with the approximate number of ovulations in the way previously mentioned for ovaries.

Immature oviducts are considerably smaller than regressed adult oviducts. The mean weight of nine immature oviducts taken from late November to late February was 0.280 gm. This figure contrasts the mean oviduct weight for wintering adults (0.743 gm.) as given in table 4.

*Recrudescence.*—It is difficult to delimit accurately the period of time involved in female recrudescence. The most complicating factor appears to be migratory movement which brings into the study area birds of varying degrees of development. This point was discussed earlier in the section on male recrudescence.

The recrudescence of females appears to lag behind that of males in most cases.



TABLE 5  
MEASUREMENTS OF OVARIES AND OVIDUCTS OF MALLARDS IN REGRESSION

Class of female	Specimen number	Days of regression	Ovary weight (gm.)	Largest follicle (mm.)	Oviduct weight (gm.)	Oviduct length (mm.)
Incubating hens <sup>1</sup>	63	5	0.415 <sup>2</sup>	4.7	5.806	140
	7	9	1.232	5.5	4.325	120
	58	11	1.302	7.0	4.184	130
	56	15	0.953	6.1	3.010	105
	62	20	0.352	3.4	2.979	100
Brood hens <sup>3</sup>	16	25	0.236	2.3	2.013	100
	17	25	0.216	1.9	1.488	80
	6	28	0.371	2.6	2.125	80
	8	32	0.505	3.6	1.440	85
	14	32	0.182	2.0	1.474	85
	11	45	0.168	1.6	1.507	90
	10	53	0.246	2.4	1.286	95
	18	57	0.125	1.7	1.334	85
	12	59	0.208	1.8	1.643	90
	13	73	0.182	2.1	1.551	90
	15	88	0.167	1.7	1.031	85

<sup>1</sup> The regressive period of incubating hens was determined by comparison of the embryos with a preserved series of known age, or by incubating the clutch in an electric incubator (total period of incubation assumed to be 23 days).

<sup>2</sup> Although it did not appear damaged, there is a possibility that part of this ovary was lost during collection; the weight does not seem to fit the trend indicated by the other figures.

<sup>3</sup> The regressive period of brood hens was determined by allowing 23 days for incubation, and then adding the age of the brood to this figure. Brood age was estimated by careful analysis of collected young according to the criteria established by Southwick (1953) and by Gollop and Marshall (1954).

One aspect of the time lag can be gathered from 11 instances in which both members of a pair were collected and in which the hen was either intermediate or gravid (table 4) in reproductive development. Among the 11 drakes, five were in full sexual maturity (Stage 6); three were nearing maturity (Stage 5); the remaining three were in stages 2, 3, and 4, respectively. Höhn (1947) found recrudescing male Mallards two to three weeks in advance of females. Both Kirkpatrick (1944) and Hiatt and Fisher (1947) show similar findings with respect to the Ring-necked Pheasant (*Phasianus colchicus*). The timing difference between males and females in the present study appears to be much the same as reported by the above authors. As previously mentioned the general recrudescence of males in this region begins in late December and early January. On this basis, most females probably start recrudescing by mid- to late January. The gradual enlargement of follicles on the immature ovary was discussed earlier. This growth pattern appears to bring the immature ovary to the developmental level of the regressed adult structure by the time that rapid recrudescence gets under way.

It appears that the initial recrudescence to breeding condition is a gradual phenomenon requiring about two months. An amazingly fast recrudescence development can apparently take place subsequent to this first gradual phase. Sows (1955) shows re-nesting by two female Pintails (*Anas acuta*) following loss of newly hatched broods. These birds re-nested in 16 and 18 days, respectively. As will be shown in the next section, the ovaries of these two hens must have been almost completely regressed, and it seems remarkable that they were able to regain sexual capacity in such a relatively short period.

*Regression.*—Table 5 compiles measurements of ovaries and oviducts from a group of females in which the regressive periods could be accurately estimated. The data from table 5 are graphed in figure 3.

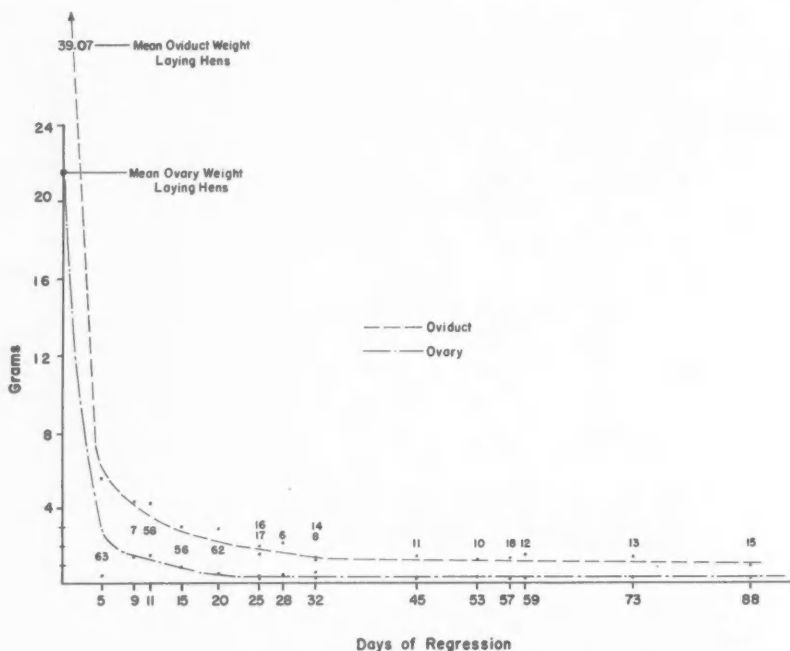


Fig. 3. Weight regression of ovaries and oviducts of Mallards. Numerals refer to specimen numbers.

The close correlation between ovary and oviduct regression, and the exceedingly fast regressive rate during a short period immediately following the start of incubation, are clearly indicated by the graph. In the first five post-incubation days, about 85 to 90 per cent of ovarian regression was completed (allowing slightly higher weight for the five-day ovary), and around 85 per cent of oviducal regression. Meyer, Kabat, and Buss (1947) found that there was very rapid follicle regression in pheasants during the first 36 to 48 hours after incubation began. They report slower regression from the second to the fifth day, and extremely slow regression by the seventh or eighth day. Although they give no figures on total weight of ovaries, it is logical that the trend of follicle regression would be similar to that of weight regression. On this basis, it is very possible that the initial regression in the Mallard is even faster than my data show. At any rate, it is evident that the major part of ovarian and oviducal regression takes place over a very short period immediately after incubation begins.

The time required for complete ovarian regression to winter weight levels (table 4) was varied. Two hens reached such a point after 25 days. By 53 days, all birds appeared to be thoroughly regressed. Considering individual variations, it appears that complete ovarian regression is accomplished in from 25 to 50 days after the onset of incubation.

Weight regression of the oviduct is slower than that of the ovary. Fairly large weight losses are evident during the first 25 to 30 post-incubation days, but after this, losses appear to be very gradual. The 88-day oviduct was approaching complete regression.

It seems likely that at least 100 days are required for regression to the winter level indicated in table 4. Oviduct length does reach winter levels by 25 to 30 post-incubation days, indicating that further weight losses are dependent upon a thinning through continuing resorptive processes.

The regressive pattern of ovary and oviduct resembles that already discussed for testes, in that a two-stage sequence seems evident. The first stage accomplishes the vast majority of regressive change over a relatively short period. The second stage is much more gradual.

#### SUMMARY

Mallards (*Anas platyrhynchos*) were found to retain remnant bursae. It could not be determined whether these structures are characteristic of yearling birds or are retained indefinitely. Comparative weight and size measurements of both mature and remnant bursae are given.

The testes of 86 Mallards were studied microscopically and placed within a classification consisting of seven histologic stages representative of the entire annual cycle. Histologically mature testes were found in breeding males and also in males which had recently deserted their breeding territories. Some males retain mature gonads during the early stages of the postnuptial molt. The degenerative process of testicular regression begins early in the postnuptial molt period and persists into the prenuptial molt period. The testes appear to be completely regressed by the time that complete prenuptial plumage is acquired.

Testicular weight and size measurements are discussed. A wide range of variation in the measurements of histologically mature testes was found. This may indicate a direct relationship between gonadal hypertrophy and the length of the territorial period. Such a relationship also seems likely for laying females in which greater weight of ovary and oviduct appears to be directly correlated with the number of ovulations, and hence a longer total time of sexual stimulation. Relative age may also be an influencing factor in both sexes.

A great deal of individual variability with respect to sexual maturity was found among both males and females during the recrudescence period. Such variation is probably to be expected as a result of differing environmental conditions on wintering areas; but it may also reflect an inherent phenomenon based on racial affinities, as has been shown for certain passerines. In mated pairs, recrudescence of the female appears generally to lag behind that of the male.

Using events of the postnuptial molt as a time scale, the approximate rate of testicular weight regression was estimated. The overall regressive change appears to be a two-stage process. In the first 1.5 to 2.5 weeks of the postnuptial molt, the major part of regression takes place. Following this, testis weights decrease gradually for a variable period of from one to two months.

The penis was found to undergo a cycle paralleling that of the testes. Weight and morphology changes of the organ are discussed.

It was possible to estimate accurately the regressive periods for a number of females. There is an exceedingly fast regression of both ovary and oviduct during the first few days following the start of incubation. Complete regression of the ovary appears to be accomplished more quickly than that of the oviduct.

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## PTERYLOSIS OF THE MALLARD DUCK

By PHILIP S. HUMPHREY and GEORGE A. CLARK, JR.

Although several studies of the distribution of feathers on the wing and other parts of various species of the Anatidae have been made, there is no general account of the pterylosis of any one species.

The present study is a preliminary attempt to describe the general pterylosis of the Mallard (*Anas platyrhynchos*). Much yet remains to be done. It would be most desirable to delimit more precisely the extent of variation in number and distribution of feathers in various tracts. Attempts should be made to comprehend the geometry underlying the distribution of the minute feathers of the head, neck, and other regions of the body. The great abundance of feathers on the Mallard (Knappen, 1932, counted 11,903 contour feathers on a female) accounts for an unevenness in our treatment: the larger, more prominent and less numerous feathers have inevitably received more attention than the very abundant small feathers.

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## METHODS AND MATERIALS

A total of about 30 specimens was examined. This number included males and females, adults and first-year birds, and birds in molt. Most of the specimens were received alive and examined soon after they were anaesthetized. These were subsequently preserved in formalin and re-examined.

In describing each feather tract we made detailed examinations of two or three specimens and attempted to clarify any apparent inconsistencies by the examination of several additional specimens.

We have used several methods of examining specimens. Freshly killed, unpreserved specimens were first examined to determine direction of overlap of feathers in the alar tract. We attempted to count feather rows and feathers in each row in the intact specimens. Once the feathers had been disturbed it was difficult to determine their manner of overlap. Detailed examination of unclipped feathers was made in an attempt to relate feather orientation, shape, size, color, and pattern to the arrangement of intersecting feather rows.

Following examination of unclipped specimens, various tracts of feathers were clipped and the initial interpretation checked against the now more easily apparent pattern of feather rows.

Examination of the spinal and other tracts was undertaken in part using soft-ray X-rays. Drawings were traced from X-ray positive prints and then compared with clipped specimens.

The relationship of some of the wing feathers to the underlying skeleton was determined by dissection.

#### ALAR TRACT

Several authors have studied the alar tract of various species of ducks; there is, however, no comprehensive discussion of this tract for any species of duck. Nitzsch (1867), Sundevall (1886; translation of 1843 paper), and Goodchild (1886; 1891) discussed some aspects of the pterylosis of the wing of *Anas*. Wray (1887) and Pycraft (1890) presented the most complete discussions of the pterylosis of the wing of *Anas*. Other papers which have an important bearing on the pterylosis of the wing of ducks are those of Gerbe (1877), Degen (1894), Reichling (1915), Steiner (1918; 1956), Bates (1918), and Verheyen (1958).

The most conspicuous feathers on the wing of the Mallard and most other birds are the REMIGES, or flight feathers. These extend from the trailing edge of the wing and are divided into two major groups, PRIMARIES and SECONDARIES. The most distal set of remiges, the primaries, are attached to the skeleton of the hand. The secondaries are attached to the forearm and distal part of the upper arm.

Large areas of the upper and lower surface of the wing bear coverts which are arranged in rows extending the length of the wing. The rows of coverts lie more or less parallel to one another and to the row of remiges. Coverts on the dorsal surface of the wing are called UPPER WING COVERTS; those on the ventral surface are termed UNDER WING COVERTS. The leading edge of the wing is considered to be anterior, and the trailing edge posterior. The most anterior of the wing feathers are the MARGINAL COVERTS; these are largely confined to the leading edge of the wing. In general, the most anterior rows of wing coverts contain the smallest feathers; posteriorly the feathers become progressively larger. The most posterior feathers, the remiges, are for the most part the largest feathers of the wing. Exceptions to this general rule are certain large marginal coverts along the anterior margin of the ventral surface of the propatagium (cf. Fürbringer, 1902:pl. 20) and ALULA QUILLS and their coverts.

In addition to the remiges, coverts, and alula quills, the wing bears two other sets of feathers: the POSTHUMERALS, attached to the dorsal surface of the upper arm, and the AXILLARIES, attached to the ventral surface of the upper arm.

The feathers of the wing are for the most part arranged in a grid comprising rows extending proximo-distally and, roughly at right angles to these, rows running approximately antero-posteriorly. The remiges, comprising the most prominent row of wing feathers, form the basis for the nomenclature of most of the feathers of the forearm and hand. However, the remiges have been interpreted as being a composite row which comprises parts of what may have been two distinct rows earlier in the phylogeny of the wing. One or more additional rows of wing feathers are also thought to be of composite origin (see discussion of diastatixy). If this is true, as Steiner (1918; 1956) and others believe, then discussion of the possible homologies of feathers or groups of feathers is potentially confusing from the nomenclatorial standpoint. One could discuss the possible homologies and names of parts of feather rows in terms of their presumed ancestral or developmentally precursor positions although the current shortage of information makes

this inadvisable. We have chosen not to attempt this. Instead we have named feathers—sometimes perhaps arbitrarily—in terms of our understanding of the geometry of the adult wing. In short, we have been content to try to follow the established nomenclature, which attempts to relate feathers and rows of feathers to the pattern as seen in the adult wing.

We have used several sources of evidence in deciding what names to apply to feather rows or parts of feather rows:

1. Relation to geometry of feather row grid
  - a. Relation to antero-posterior row
  - b. Relation to proximo-distal row
2. Relation to morphology of wing
3. Feather morphology
  - a. Feather shape
  - b. Feather size
  - c. Feather pattern and color
4. Feather orientation
  - a. Direction of feather shaft
  - b. Overlap
  - c. Reversal
5. Relative stage of growth of developing feather

*Primaries.*—The Mallard has eleven primaries, numbered from 1 to 11, proximal to distal. The most distal primary (the REMICLE) is very much reduced and markedly different in shape from the ten, more proximal primaries. This eleventh primary is a stiff, lanceolate feather with narrow vanes. It is not superficially visible on either the dorsal or the ventral surface of the wing, being covered dorsally by the tenth greater upper primary covert and ventrally by the tenth and eleventh greater under primary coverts.

The ventral surface of each of primaries 1 through 9 overlaps the dorsal surface of the next distal primary; the tenth primary does not overlap the eleventh.

We have used the more conservative system for numbering the digits of the manus (digit I=pollex; digit II=main digit, bearing the majority of the primaries; digit III=a reduced digit bearing primary No. 7). Montagna (1945) has concluded that digits II, III, and IV are retained in the avian wing, but the evidence for this view is not sufficiently convincing.

Primaries 1 through 6 are attached to the dorsal surface of the carpometacarpus and have been called METACARPAL PRIMARIES (see figs. 1, 2). The calami of the five most proximal metacarpal primaries pass over the intermetacarpal space from the dorsal surface of metacarpal II. The calamus of the sixth primary passes over the proximal border of the distal METACARPAL SYMPHYSIS from the distal end of metacarpal II. The seventh primary is attached to the single phalanx of digit III and has been termed the AD-DIGITAL PRIMARY. Primaries 8 and 9 are attached to the proximal phalanx of digit II and have been named the MID-DIGITAL PRIMARIES. The tenth and eleventh primaries are attached respectively to the second and distal phalanges of digit II and have been called collectively the PRE-DIGITAL PRIMARIES. The distalmost pre-digital primary (the eleventh) is the remicle.

*Greater upper primary coverts.*—The Mallard has eleven greater upper primary coverts, numbered 1 to 11, proximal to distal. Each of these feathers lies distal to the primary with which it is associated; neither the calamus nor the rachis of any given greater upper primary covert crosses the calamus or rachis of its associated primary remex. The greater upper primary coverts overlap one another in the same manner as do

the primaries ("conforming overlap," cf. Bates, 1918:532-533; "contrary overlap" of coverts is overlap opposite to that of the remiges).

The tenth greater upper primary covert is somewhat reduced (about three-fifths the length of the ninth) and lanceolate in shape. The eleventh greater upper primary covert is even more reduced than the tenth (about a third the length of the ninth) and is not lanceolate. Petrides (1943:264) noted that in *Anas* the outermost greater upper primary covert was small but of easily visible size (type 2 of Petrides). Measurements of these feathers were made from the point at which the calamus leaves the skin to the tip of the feather.

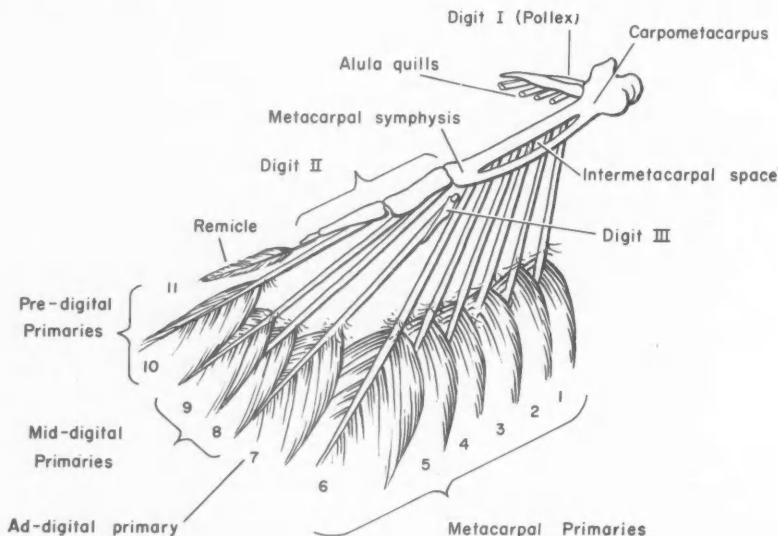


Fig. 1. The relations of wing bones and primaries in the Mallard (*Anas platyrhynchos*). Ventral view. (After Wray, 1887.)

**Middle upper primary coverts.**—Our first counts of middle upper primary coverts seemed to show that the Mallard has eleven feathers in this series. However, examination of a young specimen with partly grown wing feathers leads us to conclude that the Mallard has only ten middle upper primary coverts. These are numbered 1 to 10 from proximal to distal along the manus to correspond with the numbering of the primaries and their greater upper coverts (fig. 2).

Because of crowding at the distal end of the wing, it is difficult in some cases to determine to which proximo-distal row a particular feather belongs. In the young specimen the middle upper primary coverts protrude 14 or 15 millimeters from their sheaths. The questionable eleventh middle upper primary covert protrudes only 3 millimeters from its sheath. In this respect, as well as in coloration, it resembles the more proximal feathers in the marginal series along the leading edge of digit II. The position of this distalmost marginal feather is appropriate for an eleventh middle upper covert; however, this feather is sufficiently different from the middle upper primary coverts in color and stage of growth that we consider it to be a marginal covert.



The calamus of each middle upper primary covert lies distal to that of its corresponding greater upper primary covert. The middle upper primary coverts have conforming overlap.

The first middle upper primary covert is considerably reduced compared to the more distal members of the series; it is approximately three quarters the length of the second. The tenth middle upper primary covert is approximately the length of the ninth but has somewhat narrower vanes.

<div> <div>PRE-DIGITAL PRIMARIES</div> <div>MID-DIGITAL PRIMARIES</div> <div>AD-DIGITAL PRIMARY</div> <div>METACARPAL PRIMARIES</div> <div>REMICLE</div> </div>												
	No.	1	2	3	4	5	6	7	8	9	10	11
PRIMARIES	11	carpometacarpus						digit III	prox. phal. digit II		2nd phal. II	distal phal. II
Greater UPPER PRIMARY COVERTS	11	+	+	+	+	+	+	+	+	+	+	+
Middle UPPER PRIMARY COVERTS	10	+	+	+	+	+	+	+	+	+	+	-
Lesser UPPER PRIMARY COVERTS	7-9	+/-	+/-	distal to bases of greater upper primary coverts 3,4,5,6,7,8						+/-	-	-

Fig. 2. Occurrence and distribution of feathers on the dorsal surface of the manus in the Mallard; + indicates presence of feather, - indicates absence of feather.

*Lesser upper primary coverts.*—There is apparently individual variation in the number of lesser upper primary coverts in the Mallard. We have examined wings with seven, eight, and nine lesser upper primary coverts (fig. 2). In the case of nine lesser primary coverts these correspond to primaries 1 through 9 and are numbered accordingly. When less than nine lesser upper primary coverts were found, the feathers were missing at either or both ends of the row. We do not know whether these variations from the maximum count are due to accidental or natural (molt) loss of a feather or feathers.

Each lesser upper primary covert originates slightly distal to its corresponding middle upper primary covert. The lesser upper primary coverts have conforming overlap.

*Carpal remex and its coverts.*—The carpal remex in the Mallard is a somewhat degenerate, down-like feather with a very fine, almost hair-like rhachis. It is approximately 3 centimeters in length, measured from its apex to the point at which the calamus enters the skin. A gap, or DIASTEMA, at the wrist joint separates the row of primary remiges on the manus from the row of secondary remiges on the forearm. The insertion of the carpal remex is located 2 or 3 millimeters proximal to the skin-covered calamus of the first primary. Extending from the first secondary to the insertion of the carpal remex is a fold of skin known as the PLICA SEMILUNARIS, which bridges the diastema of the wrist joint (Lowe, 1931:509).

The GREATER UPPER CARPAL REMEX COVERT originates 2 or 3 millimeters anterior and slightly distal to the point at which the calamus of the carpal remex inserts in the skin. The greater upper carpal remex covert is a well-developed feather similar in size and shape to one of the distal middle upper secondary coverts; it is approximately 4.5 centimeters in length from its apex to the point of insertion in the skin.

About 4 to 6 millimeters anterior to and slightly distal to the point where the calamus of the greater upper carpal remex covert disappears into the skin, there arises a MIDDLE UPPER CARPAL REMEX COVERT. This feather has the same relation to the carpal remex and its greater upper covert as do the middle upper primary coverts to their respective primaries and their greater upper coverts. The middle upper carpal remex covert is about 3.5 centimeters in length and comparable in shape and development to the underlying greater upper covert.

Prior to Degen's paper (1894) on the carpal remex and its covert, Wray (1887), Gadow (1891), and others did not distinguish these feathers from the series of greater and middle upper primary coverts. The carpal remex and its covert were considered to be the most proximal of the upper primary coverts; that is, they were thought to be coverts for the first primary. All the greater and middle upper primary coverts were thought to lie proximal to their respective primaries. According to this early system of counting greater and middle upper primary coverts (see fig. 3A), the second middle upper primary covert is missing in the Mallard (Gadow, 1891:558).

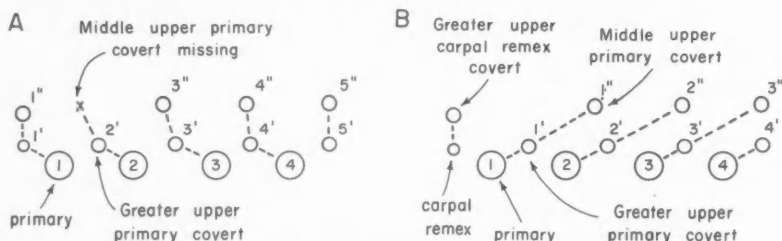


Fig. 3. A, nomenclature of the proximal primaries, their coverts, and the carpal remex, according to Wray (1887). B, current nomenclature of the proximal primaries, their coverts, and the carpal remex.

Degen demonstrated that what had been considered the greater and middle upper coverts of the first primary were really a highly modified remex and its greater upper covert. Furthermore, he presented evidence that the carpal remex and its covert are more closely allied to the secondary remiges and their coverts than to the primaries. Under Degen's system the upper primary coverts are located distal to their respective remiges. According to this revised system, the second primary does not lack a middle upper covert (see fig. 3B).

With regard to ducks, Degen (1894:xiv-xv, fig. 4) stated: "In the *Anatidae* the disputed 'covert' [= carpal remex] is placed midway between the metacarpals [= primaries] and the cubitals [= secondaries] . . . The space between these two series of feathers is greater in the Ducks than in any other birds with which I am acquainted, and is far in excess of the interspace between any two of the cubital [= secondary] remiges. In the wing of *Dendrocygna* . . . the position of the 'covert' is seen to perfection . . . Here we find the 'covert' resting on the metacarpus, leaving the carpus proper free from contact with any flight-feather. Its position is seen in the figure just referred to [Degen's figure 4], and its independence from the 1st metacarpal [= primary No. 1] is established."

Figure 4 of Degen's paper (1894) shows the relationship of the carpal remex to other nearby feathers on the dorsal surface of the wing of a Mallard.

Boulton (1927:392, 397) reported an under carpal remex covert in the House Wren (*Troglodytes aedon*), but Van Tyne and Berger (1959:81) have commented that "the homology seems uncertain at best."

*Diastataxy*.—Gerbe (1877) was apparently the first to note the absence of the fifth secondary in various birds including the *Palmipedes* (which presumably contained the *Anatidae*); the coverts for this missing secondary were found to be present. Goodchild (1886) reported the occurrence of an accessory row of upper secondary coverts on the dorsal surface of the wing in ducks; the presence of this accessory row may be interpreted as supporting Steiner's (1918) explanation of the absence of the fifth secondary. Wray (1887:345) noted the absence of the fifth secondary in the duck and termed this the "aquantocubital" condition. Wray (1887:350) found the fifth secondary absent in young ducklings as well as in adult birds. Pycraft (1890:127) noted in the Mallard an interruption of the row of middle upper secondary coverts above the region of the missing secondary. Degen (1894:xix) expressed the view that there was a possibility of finding a vestigial form of the fifth secondary. He presented an elaborate hypothesis to explain the absence of the fifth secondary. Degen postulated that during the phylogenetic history of diastataxic birds there was a relocation of feathers from the third and fourth digits to the ulna. He suggested that in the course of this transfer of feathers to the ulna, the fifth secondary was lost.

Mitchell (1899) proposed the terms "diastataxic" to replace "aquantocubital" (absence of the fifth secondary) and "eutaxic" to replace "quintocubital" (presence of the fifth secondary). These terms were suggested in connection with his opinion that the diastataxic gap did not represent a phylogenetic or ontogenetic loss of a secondary. Mitchell described the wings of certain pigeons which were essentially eutaxic except for the presence of two (instead of the usual one) greater upper secondary coverts over the closed diastataxic interspace. He believed that the eutaxic condition was secondarily evolved from the diastataxic arrangement. Mitchell postulated that diastataxy originated from shifts of rows of scales or feathers in a hypothetical pentadactyl wing. According to Mitchell, the eutaxic condition was formed from the diastataxic condition by a closing of the gap.

Pycraft (1899), on the basis of a study of the anatomy of the wings of embryos, including those of the Mallard, argued that diastataxy did not involve the loss of a fifth secondary but merely the embryonic downward rotation of the four most distal feathers of the forearm resulting in the apparent absence of a fifth secondary. The downward rotation of the distal secondaries and their associated coverts was thought to result possibly from a slight lengthening of the forearm. According to Pycraft, the eutaxic condition was phylogenetically and ontogenetically primitive. The diastataxic condition came later in the evolutionary and developmental sense and did not involve the loss of a secondary. Certain eutaxic forms such as some kingfishers, swifts, and pigeons were thought by Pycraft (1899:254) to be secondarily derived from diastataxic ancestors. Pycraft (*op. cit.*:246) mentioned briefly an otherwise unpublished hypothesis of E. S. Goodrich to account for diastataxy. Goodrich thought that the diastataxic condition could have arisen through the bifurcation of a row of feather papillae, probably those of the greater upper secondary coverts 1 through 5.

Steiner (1918, 1956) presented additional hypotheses to account for the diastataxic and eutaxic conditions. He (1918:254) showed that the diastataxic condition is already present with the first appearance of feather papillae in the embryonic duck. Steiner believed that the diastataxic condition arose phylogenetically through the upward rotation of the five distalmost feathers of each of several feather rows on the posterior margin of the distal end of the forearm (see fig. 4). He presented data indicating that in phylogeny the eutaxic condition is secondarily derived from the diastataxic condition.

Representations of Steiner's hypotheses on the origin of diastataxy by Miller (1941:

114) and others (cf. Van Tyne and Berger, 1959:81-82) do not correspond with Steiner's (1956:4-6) views on the subject. Steiner did not state that diastataxy arises through the shifts of parts of embryonic feather rows during the ontogeny of an individual bird. Steiner (1918:446-447) made the following statements (translated from German):

"If we do not make the completely improbable assumption that diastataxy was formed several times independently and always by coincidence in the fifth or rather sixth [including the carpal remex and coverts] transversal row, then there is no choice but to assume that it was acquired by one ancestor common to all birds . . . Most probably the transformation of the reptilian forelimb into the bird's wing caused the formation of diastataxy."

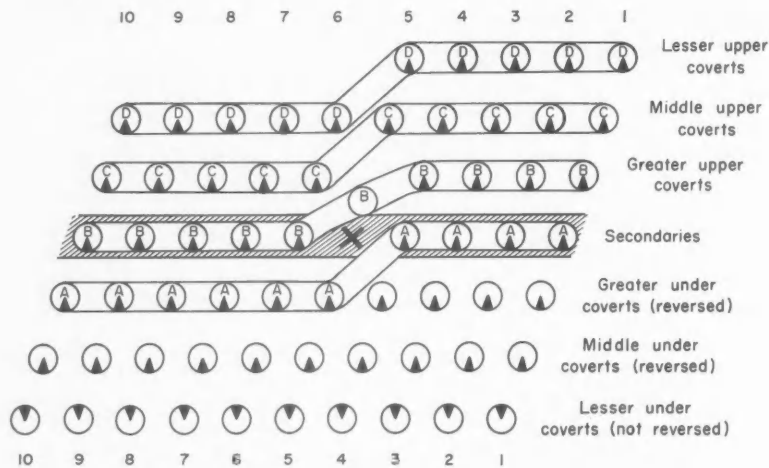


Fig. 4. Graphic representation of Steiner's hypothesis on the phylogenetic origin of diastataxy. Letters indicate ancestral rows.

Verheyen (1958) has developed the most recent hypothesis to explain the diastatic condition. According to him, in diastatic birds the fifth greater under secondary covert is homologous with members of the secondary series. All rows but the fifth transversal (antero-posterior) row have moved from ventral to dorsal in diastatic wings. The fifth transversal row does not move because the fifth lesser under secondary covert is attached to the radius by a ligament, thus effectively immobilizing the entire row. Eutaxy is thought to result from the weak development or absence of this ligament.

Steiner's hypotheses raise problems concerning the homology and nomenclature of secondaries and their coverts. The secondaries are a functional row which is derived, according to Steiner, from two phylogenetically precursor rows. This is illustrated diagrammatically in figure 4. According to Steiner, neither diastatic nor eutactic birds have ever had a fifth secondary. The apparently "missing" fifth secondary is represented by the fifth greater upper covert. The numbering system used by Steiner for the secondaries and their coverts is a practical one. In diastatic birds the diastatic gap is counted as a fifth position in the row of secondaries. Some authors (for example, Van Tyne and Berger, 1959:82) assign the number "5" to the secondary proximal to

the diastataxic interspace; such a numbering system has the unfortunate disadvantage that the secondaries do not have the same numbers as their associated coverts.

In the eutaxic bird, according to Steiner's scheme, secondaries homologous to 4 and 6 of the diastataxic wing come together (during phylogeny) closing the diastataxic gap.

The relationship of the practical numbering system of feather rows (as seen in the adult wing) to the original rows as hypothesized by Steiner is shown in figure 4.

*Secondaries.*—As found by Wray (1887:pl. 29), there are 18 secondaries in the Mallard (some individuals have 17 secondaries). An apterium is present on the proximal end of the secondary series and continues proximally into the axilla. The secondaries are numbered from 1 to 19 from distal to proximal. There is a conspicuous gap between secondaries 4 and 6; this diastataxic condition has long been known for the Anatidae (Gadow, 1891:567).

Secondaries number 1 through 12 (exclusive of the nonexistent number 5) are ordinary secondaries; they are approximately equal in length and bear the "speculum." Numbers 10, 11 and 12 are longer than any of the more distal secondaries. Number 12 is longer than number 11 which is longer than 10. Secondaries 13 through 16 are all longer than any in the secondary series 1 through 12. Numbers 13 through 16 are elongate, rather pointed feathers. Secondaries 14 and 15 are the longest of the secondaries. Proceeding proximad from secondary number 16, the secondaries become progressively and rapidly much shorter. Secondary number 13 is somewhat pointed; number 14 is more pointed. Numbers 15, 16, and 17 are very pointed. Number 18 is slightly rounded at the tip. Number 19 (when present) is more rounded at the tip than is 18.

*Greater upper secondary coverts.*—The number of greater upper secondary coverts in the Mallard seems to vary between 19 and 20. We are not certain how variable this count may be since these feathers are difficult to identify accurately in the region of the elbow. These coverts are numbered to correspond with their appropriate secondaries except in the case of the fifth covert for which there is no corresponding secondary. In those individuals in which secondary number 18 is the proximalmost of the series, greater upper secondary covert 19 is present; those in which secondary number 19 is present have a greater upper secondary covert number 20. The rachis of each of the greater upper secondary coverts for which there is a secondary lies distal to the rachis of its respective secondary. Greater upper secondary coverts 1 through 13 have conforming overlap. Greater upper secondary covert number 14 overlaps both 13 and 15 and marks the beginning of contrary overlap which persists to the proximalmost of the greater upper secondary coverts. In the fully spread wing, greater upper secondary coverts 1 through 5 appear to be two or three millimeters longer than the rest of the series.

*Middle upper secondary coverts.*—Each of the 19 middle upper secondary coverts originates distal to its respective greater upper secondary covert. The fourth middle upper secondary covert is the longest. With some irregularity, there is a tendency for middle upper secondary coverts to be progressively shorter on either side of the fourth middle upper secondary covert. The middle upper secondary coverts have contrary overlap distally; proximally, in the region of the elbow, overlap is conforming (Wray, 1887:345).

The five distal middle upper secondary coverts form a row which is not directly continuous with any other row of feathers. See figure 5, which diagrammatically shows the arrangement of the upper secondary coverts. This row of five distal middle upper secondary coverts is an extra row such as might be expected according to Steiner's (1918) hypothesis on the origin of diastataxy.

*Lesser upper secondary coverts.*—As is indicated in figure 5, there are four rows of lesser upper secondary coverts. These rows extend varying distances along the forearm. Proximally they are in contact with the rows of marginal coverts covering the dorsal surface of the patagium. The three most posterior rows of lesser upper secondary coverts are at their proximal ends separated from the marginal coverts of the patagium by an apterium lying over the elbow joint. Distally the upper surface of the forearm becomes narrower, and the rows of lesser upper secondary coverts merge with the marginal coverts of the leading edge of the wing.

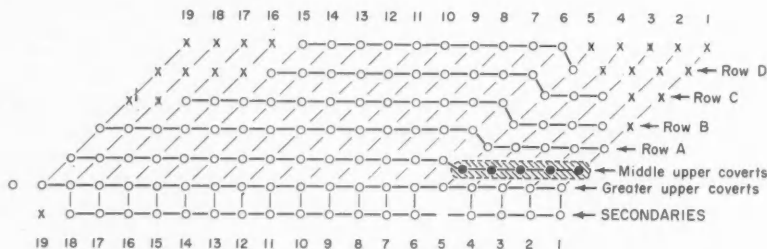


Fig. 5. Diagrammatic representation of the distribution of feathers on the dorsal surface of the forearm in the Mallard, showing the secondaries, their upper coverts, and the so-called accessory row (shaded).

Lesser upper secondary coverts lie distal to their respective middle upper secondary coverts. Distally on the forearm, the overlap of the lesser upper secondary coverts is contrary.

In one specimen there were 19 feathers in row A of the lesser upper secondary coverts. In row B, coverts number 1, 18, and 19 were absent; in row C, coverts 1, 2, and 16 through 19 were absent; in row D, coverts 1 through 4 and 16 through 19 were absent (see fig. 5).

*Under wing coverts.*—Sundevall (1886:418–419) noted the so-called reversed under coverts of birds. The reversed coverts lie on the ventral surface of the wing but have an orientation like that of the feathers on the dorsal side of the wing. Sundevall distinguished the reversed feathers by means of the orientation of the grooved shaft and other points of feather structure. He hypothesized that the reversed feathers were merely strongly developed aftershafts of typical feathers in which the usual development of the normal feather had been suppressed.

Wray (1887:345) noted that the greater and middle under secondary coverts of the duck's wing were reversed. He criticized Sundevall's hypothesis on the origin of the reversed under coverts and presented evidence (*op. cit.*:353–354; figs. 1 to 5 of pl. 32) that during ontogeny the two rows of reversed under coverts first appear on the dorsal surface of the wing and are later carried to the ventral surface.

Bates (1918:534–536) described the reversed under coverts of *Pteronetta hartlaubi* (Anatidae) and many other birds.

The two rows of reversed under coverts in the Mallard show no indication of having been affected by the development of the diastataxic condition; that is, there is no displaced row of five distal under secondary coverts. If Steiner's (1918) hypothesis is correct, the reversed under wing coverts presumably appeared later in anatid phylogeny than did the diastataxic condition.

*Greater under primary coverts.*—The 11 greater under primary coverts are numbered from 1 to 11, proximal to distal. Each lies proximal to its respective primary. The tenth and eleventh greater under primary coverts are moderately reduced. The eleventh greater under primary covert is about 30 mm. in length (measured from point of insertion in the skin to the tip of the rhachis) and is about three quarters the length of the tenth.

All of the greater under primary coverts are reversed; in each the superior umbilicus is on the exposed surface of the feather shaft. The calami of greater under primary coverts 1 through 5 lie each on the ventral surface of the calamus of its respective primary. The calami of greater under primary coverts 6 through 11 lie each on the proximal side of the calamus of its respective primary. The greater under primary coverts exhibit conforming overlap.

*Middle under primary coverts.*—According to W. deW. Miller (1919:563), "in the Anseres the standard number of middle primary coverts on the under side of the wing is six." In the Mallard, middle under primary coverts 1 through 6 are present; each lies slightly proximal to its corresponding greater under primary covert. The six coverts are reversed and exhibit contrary overlap.

*Lesser under primary coverts.*—There are two rows of lesser under primary coverts. We have assigned the letter "A" to the posterior row (the row closest to the trailing edge of the wing) and the letter "B" to the more anterior row. Row A has 11 feathers; row B has 10. Row B might be included among the marginals since it lies close to them, but we have arbitrarily included it with the lesser under primary coverts. The calami of row A originate proximal to those of their respective middle under primary coverts.

Neither row A nor B has reversed feathers; both rows have contrary overlap.

*Greater under secondary coverts.*—In two specimens we counted 17 greater under secondary coverts; in another specimen we counted 18 with a possible nineteenth. Pycraft (1890:128) reported that there were no greater under secondary coverts for the eighteenth and nineteenth secondaries.

The greater under secondary coverts are numbered, starting with number one, distal to proximal. Each greater under secondary covert (except the fifth) originates proximal and ventral to its corresponding secondary. The greater under secondary coverts have conforming overlap and are reversed.

*Middle under secondary coverts.*—In one specimen 17 middle under secondary coverts were found; each inserts proximal to its respective secondary and its associated greater under covert. The middle under secondary coverts are reversed and exhibit contrary overlap. Sundevall (1886:419) noted the difference in mode of overlap between the greater and middle under secondary coverts.

*Lesser under secondary coverts.*—There are five rows of lesser under secondary coverts distributed along the ventral surface of the wing from the elbow to the wrist. Pycraft (1890:129) reported four rows of lesser under secondary coverts. Wray (1887:347) and Pycraft (1890) noted the relatively great separation between the second and third rows as counted posterior to anterior.

From posterior to anterior the rows of lesser under secondary coverts have been assigned the letters A through E. None of these coverts is reversed. Lesser under secondary covert rows A, B, C, and D exhibit conforming overlaps. Overlap could not be determined for row E because the feathers in this row are rather widely separated.

The following feather counts for the five rows of lesser under secondary coverts are based on examination of two clipped wings: row A, 17; row B, 16; row C, 14; row D, 14 or 15 (uncertain); row E, 10 or 11 (uncertain). Some arbitrary allocation of feathers to particular rows was necessary for rows D and E.

*Posthumeral.*—The feather rows along the caudal margin of the skin covering the humerus are termed the posthumeral region of the alar tract. The distalmost feather of this series lies proximal to the proximalmost secondary. The series terminates proximally at the caudal end of the scapulohumeral tract. The feathers which we term posthumeral (nomenclature of A. M. Lucas, MS) are termed tertiaries by Compton (1938:201-202), humerals by Wray (1887:347) and Pycraft (1890:126-127). The term "tertiaries" has also been used for the proximalmost secondaries (Dwight, 1900:89-90). The term "humeral tract" was used by Compton (1938:199) and Humphrey and Butsch (1958:13) to refer to what we call the scapulohumeral tract (see following).



We have used the term posthumeral to avoid the ambiguity of the terms "tertiaries" and "humeral."

Wray (1887:346-347) was of the opinion that the posthumerals are continuous with the lesser upper secondary coverts; this view perhaps stemmed from the apparent correspondence of the posthumerals to the axillaries, a group of feathers on the ventral surface of the wing. (The axillaries were believed to be continuous with the lesser under secondary coverts.) Pycraft (1890:127, 138-139) thought that the posthumerals were continuous with the greater upper secondary coverts. Compton (1938:202) stated that in Falconiformes, the posthumerals are continuous with the lesser upper secondary coverts.

The posthumeral region of the alar tract and the scapulohumeral tract come together at the posterior distal margin of the scapulohumeral tract. The feathers of the two groups blend in this region so that the distinction between scapulohumeral tract and posthumeral quills is arbitrary. We were able to count 11 posthumeral quills; only six of these are prominent feathers. Counting proximal to distal, numbers 4 through 9 are the prominent posthumeral quills.

The six prominent posthumeral feathers are overlain by greater upper posthumeral coverts. Each of these coverts originates slightly distad and 7 or 8 mm. anterior to the point at which the rhachis of the respective posthumeral quill passes from the skin. In addition to these 6 greater upper posthumeral coverts, there is possibly a seventh, distal to the others. This seventh feather is very small and quite down-like. Distal to this seventh feather is a series of little down-like feathers. These form the caudal margin of a small apterium on the dorsal surface of the elbow joint. The first three feathers distal to the possible seventh greater upper posthumeral covert are downy. The feathers of this series distal to the first three are larger and slightly more pennaceous. This last described series is possibly a continuation of the greater upper posthumeral coverts.

Ventral to the posthumerals are the under posthumeral coverts; these are separated by an apterium from the more anteriorly lying axillaries.

*Axillaries.*—Six or seven large axillaries originate on the ventral surface of the upper arm beneath the humerus. Wray (1887:347) and Pycraft (1890:138-139) noted that the axillary row was continuous with a row of lesser under secondary coverts. As Pycraft noted, the axillaries are not reversed in their orientation, unlike the greater and middle under secondary coverts.

There are two complete rows of under axillary coverts and, most anteriorly, a third partial row. Row A is the first row anterior to the axillary row. Row B is the next row anterior. Row B is apparently continuous with a row of the lesser under secondary coverts. The calamus of each of the feathers in row A originates proximal to its respective axillary. The partial row C of under axillary coverts is found anterior to the four most proximal of the axillaries.

An apterium lies anterior to row C of the under axillary coverts and to the distal end of row B of the under axillary coverts. Anterior to this apterium lie the marginal coverts of the ventral side of the upper arm. Posteriorly the axillaries are separated from the under posthumeral coverts by an apterium which is located on the postero-ventral surface of the upper arm.

*Alula.*—In the Mallard there are five alula quills, each with its own greater covert. Wray (1887:347) reported that there were four alula quills, each with a covert; he apparently did not count what we consider the most proximal of the alula quills.

The five alula quills are numbered 1 to 5 proximal to distal along the pollex. The alula quills become progressively longer going proximal to distal. The most proximal



or first alula quill stands in the proper relation to the middle upper carpal remex covert to be considered as possibly a lesser upper carpal remex covert.

Degen (1894:xxix) recognized greater, middle, and lesser upper coverts on the alula. He also reported two reversed greater under coverts on the alula; we found one such reversed covert. Degen believed the alula quills were true remiges; Wray (1887:347) thought the feathers of the pollex were derived from the marginals and the lesser upper coverts of the primaries.

*Marginal coverts.*—The marginal coverts are arranged in several rows along the leading edge of the wing. Due to the small size of these feathers and their dense arrangement, we have not attempted to study this region on a feather by feather basis. The following is a general account of the distribution of the marginal coverts.

On the dorsal surface of the manus these feathers extend proximally from the base of the eleventh primary to an apterium lying under the alula quills. The distal margin of this apterium is marked by the anterior end of the calamus of the fourth primary. The thickly clustered marginal coverts continue proximally from the alula along the leading edge of the fore and upper arm to merge with the anterior end of the scapulo-humeral tract. On the dorsal surface of the wing the marginal region is expanded to cover the propatagium.

On the ventral surface of the wing the marginal coverts extend the length of the leading edge distal to the base of the eleventh primary. The marginal coverts on the ventral surface do not take origin from the entire propatagium but are confined to the leading edge. These marginal coverts in front of the propatagium are longer than typical marginal coverts so that they serve to conceal the apterium of the ventral propatagium (Wray, 1887:347).

#### SCAPULOHUMERAL TRACT

This tract lies dorsal to the proximal end of the humerus. Antero-laterally the scapulo-humeral tract is continuous with the sternal region of the ventral tract. Anteriorly and antero-laterally it fuses with the marginal coverts of the alar tract. The humeral apterium lies lateral to the scapulo-humeral tract ("humeral tract" of Humphrey and Butsch) which is not bounded laterally by the lateral thoracic apterium contrary to Humphrey and Butsch (1958). The lateral thoracic apterium lies adjacent to the scapulo-humeral tract only on the postero-medial edge of the latter. The humeral apterium separates the scapulo-humeral tract from the marginal coverts of the patagium. The interscapular apterium lies medial to the scapulo-humeral tract. Postero-laterally the scapulo-humeral tract is continuous with the posthumeral region of the alar tract.

The scapulo-humeral tract is a little over one centimeter in width and contains posteriorly six rows of feathers aligned antero-posteriorly. The feathers toward the posterior end of the scapulo-humeral tract are much larger than those located more anteriorly.

#### SPINAL TRACT

Our study of the pterylosis of the spinal tract of the Mallard was undertaken by attempting to compare a clipped specimen with a detailed drawing made by tracing positive prints of X-rays of a flattened skin. Our attempt was not entirely successful for several reasons: (1) the tremendous number of feathers involved made the comparison laborious and subject to error; (2) distortion of the dried skin and the fact that it had many incompletely grown feathers made the X-rays difficult to interpret; and (3) we have no way of knowing whether certain irregularities or discrepancies can be ascribed to individual variation, to our own errors of misinterpretation, or to artifacts.

Nitzsch (1867:146-148) presented a comparative account of the spinal tract of

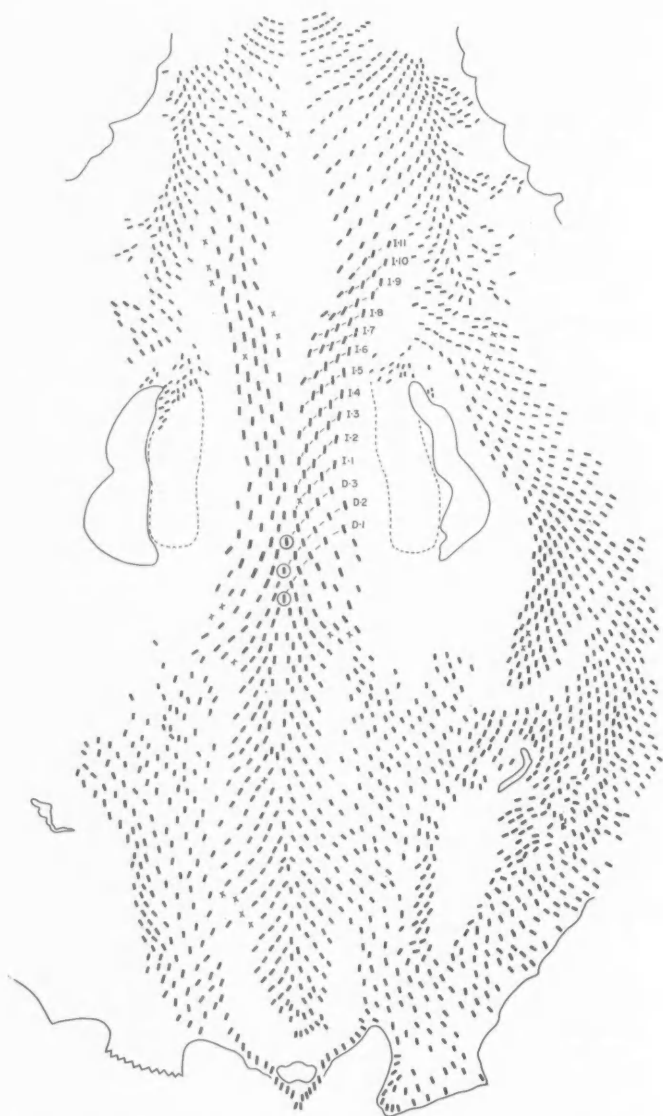


Fig. 6. Pterylosis of the trunk of the Mallard. For nomenclature see figure 7 and the text.

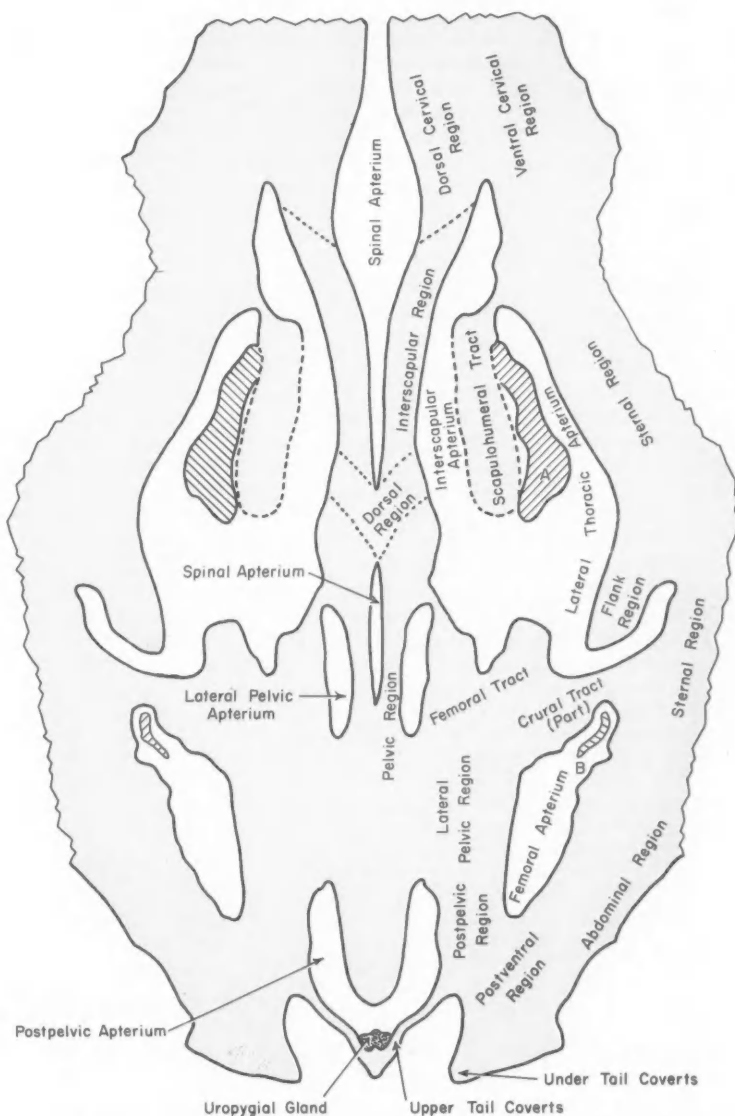


Fig. 7. Nomenclature of the feather tracts (and their regions) of the trunk of the Mallard. Feathered areas are shaded; hatched regions are holes where wings (A) and legs (B) were removed.

waterfowl (including *Anas platyrhynchos*) and noted that this tract is uniform throughout the family. He found that two characteristics of the spinal tract show interspecific variation: (1) the antero-posterior extent of the spinal apterium, and (2) the anterior extent of the so-called "lateral neck space" or lateral cervical apterium. What Nitzsch called "true ducks" correspond to the tribes Anatini, Cairinini, and Tadornini. Nitzsch characterized these as having—in common with the Aythyini, Mergini (except *Mergus*), Oxyurini, and Somateriini—(1) a longer and stronger terminal branch of the ventral tract than in swans and geese, and (2) a shorter lateral cervical apterium than in swans and geese. He stated that the lateral cervical apterium is lacking in *Mergus*. According to Nitzsch, the "true ducks" (Anatini, Cairinini, Tadornini) have a spinal apterium which extends from the base of the neck to the "caudal pit"; in other ducks it never extends much beyond the interscapular region.

Humphrey and Butsch (1958) used the X-ray method to study the spinal tract of the Labrador Duck (*Camptorhynchus labradorius*). They were unable to determine the anterior extent of the spinal apterium in this species; they made no mention of the lateral cervical apterium.

Compton (1938:183) divided the spinal tract of the Falconiformes into six regions as follows: (1) dorsal cervical, (2) interscapular, (3) lateral scapular, (4) dorsal, (5) pelvic, and (6) lateral pelvic. We include a seventh region, the postpelvic. Compton considers the postpelvic region to be a part of the caudal tract. Compton stated that the spinal tract "extends from the base of the head to the uropygial gland." We can see no clear boundaries to the spinal tract in the Mallard except (1) the lateral margins of the interscapular region, and (2) the caudal margin of the pelvic region. Otherwise, the spinal tract merges (1) anteriorly with the capital tract, (2) anteriorly and laterally with the ventral cervical region of the ventral tract, (3) posteriorly and laterally with the femoral tract, and (4) far posteriorly and laterally with the post-ventral and/or the abdominal regions of the ventral tract.

*Dorsal cervical region.*—Only the posterior part of the dorsal cervical region is shown in figures 6 and 7. The right and left parts of the dorsal cervical region become more widely separated posteriorly as the spinal apterium becomes broader. According to Compton (*loc. cit.*) the dorsal cervical region terminates at the trunk. In the Mallard this point corresponds to the anterior limit of the lateral cervical apterium.

*Interscapular region.*—The interscapular region commences anteriorly as two relatively widely separated branches which are continuations of the right and left parts of the dorsal cervical region. The anterior part of each branch of the interscapular region is bounded laterally by a narrow lateral cervical apterium. More posteriorly the lateral cervical apterium continues as the interscapular apterium, bounded laterally by the scapulohumeral tract and medially by the corresponding branch of the interscapular region. The spinal apterium becomes narrower posteriorly and terminates at an unpaired median dorsal feather. Between this point and the anterior limit of the lateral cervical apterium each branch of the interscapular region comprises eleven rows of feathers (rows I-11, fig. 6). We interpret each feather row as being oriented from postero-medial to antero-lateral. The first feather row anterior to the posterior termination of the spinal apterium consists of five feathers. Rows 2 through 8 also comprise five feathers each. Row 9 has six feathers; row 10, five; and row 11, four feathers. These counts may not be accurate in the anterior part of each branch of the interscapular region since we did not obtain the same feather row count on each side in this area.

*Dorsal region.*—We judge that the dorsal region of the spinal tract begins at the posterior termination of the interscapular part of the spinal apterium. In the Mallard the dorsal region comprises three rows of 11 feathers (D-1, D-2, D-3, fig. 6), each row comprising a row of five on either side of the midline and a median unpaired feather (encircled in fig. 6). The dorsal region is bounded laterally on each side by the posterior part of the interscapular apterium.

*Lateral scapular region.*—We were unable to distinguish a lateral scapular region.

*Pelvic region.*—The pelvic region begins anteriorly at the posterior termination of the dorsal region. The first or anteriormost six rows of the pelvic region are divided medially by a narrow apterium, a posterior extension of the spinal apterium. The seventh row has a medial unpaired feather; in the eighth row the medial feather is lacking. Rows 9 through 17 each have a medial unpaired feather. We are uncertain about the pattern of distribution of feathers in rows 18 through 21 of the pelvic region; some of the rows appear to have medial unpaired feathers.

		PRIMARY						SECONDARY							
		UPPER COVERTS			UNDER COVERTS			UPPER COVERTS			UNDER COVERTS				
		NUMBER	NUMBER	CONFORMING OVERLAP	CONTRARY OVERLAP	NUMBER	CONFORMING OVERLAP	CONTRARY OVERLAP	NUMBER	NUMBER	CONFORMING OVERLAP	CONTRARY OVERLAP	NUMBER	CONFORMING OVERLAP	CONTRARY OVERLAP
REMIGES		11							17-18						
GREATER			11	✓		11 *	✓			19-20	1-13	15-19	17-18 (19?) *	✓	
MIDDLE			10	✓		6 *		✓		19	prox- imal	distal	17 *		✓
LESSER	row A		7-9	✓		11		✓		19	"	"	17	✓	
	B					10		✓		16	"	"	16	✓	
	C									13	"	"	14	✓	
	D									11	"	"	14 <sup>or</sup> 15 <sup>?</sup>	✓	
	E												10 <sup>or</sup> 11 <sup>?</sup>	?	

\* = REVERSED

Fig. 8. Number of remiges and coverts in the Mallard.

Counting from anterior to posterior, the seventh through tenth or eleventh rows of the pelvic region are bordered laterally on each side by a narrow lateral pelvic apterium. The posteriormost five rows of the pelvic region are bordered laterally by the postpelvic apterium. The pelvic region terminates caudally at the postpelvic apterium.

*Lateral pelvic region.*—The lateral pelvic region of each side is bordered (1) anteriorly by part of the posterior margin of the lateral thoracic apterium, (2) medially by the lateral border of the lateral pelvic apterium and, more posteriorly, by the pelvic region, (3) posteriorly by the anterior limit of the postpelvic apterium and by the anterior limit of the postpelvic region, (4) laterally by the dorso-medial border of the femoral apterium and, more anteriorly, by the dorso-medial limit of the femoral tract. Except where bounded by the margins of apteria, the lateral pelvic region cannot be clearly delimited.

*Postpelvic region.*—We include the postpelvic region in the spinal tract rather than in the caudal tract (cf. Compton, 1938:197). Anteriorly the postpelvic region merges with the posterior part of the lateral pelvic region. The postpelvic region is bounded (1) medially by the lateral margin of the postpelvic apterium, (2) laterally by the femoral apterium, and (3) postero-laterally by the post-ventral and/or abdominal regions of the ventral tract.

## CAPITAL TRACT

It does not seem profitable to attempt to distinguish in the Mallard subregions of the capital tract as did Compton (1938:177-178) for the Falconiformes. There are no true apteria in the capital tract of the Mallard. Along the posterior margin of the auditory meatus there is a narrow bare region. There is no middorsal apterium and none about the eye. Body downs are present over the entire head, although their presence may be far from obvious to the unaided eye in examination of a pickled specimen.

## VENTRAL TRACT

Compton (1938:189-191) lists the following regions as comprising the ventral tract: (1) ventral cervical, (2) sternal, (3) axillar, (4) subaxillar, and (5) abdominal. We have considered the axillar region in the section on the alar tract; we were unable to distinguish a subaxillar region. We have limited the caudal tract to the rectrices, their coverts, and the uropygial gland; the postventral region is considered as a part of the ventral tract. We have given the name "flank region" to that part of the ventral tract which contains the flank feathers. This region was considered by Compton to be a part of the sternal region.

The ventral tract of the Mallard extends from the head to the under tail coverts. It is divided for most of its length by a narrow midventral apterium. The anterior limit of this apterium lies about 6 cm. anterior to the cranial crest of the keel of the sternum or approximately 3 cm. anterior to the termination of the lateral cervical apterium. The midventral apterium is approximately 1 cm. in width; anterior to the sternum the midventral apterium becomes slightly narrower then tapers to its anterior termination. Toward the posterior end of the sternal region the midventral apterium becomes slightly narrower and is somewhat less than a centimeter in width throughout the abdominal region.

The ventral tract has definite limits at (1) the lateral cervical apterium where the posterior part of the ventral cervical region and/or the anterior part of the sternal region terminates dorso-laterally; (2) the lateral thoracic apterium which provides the dorso-lateral margin for most of the sternal region and the dorso-lateral, posterior, and ventro-lateral margins for the flank region; and (3) the femoral apterium which provides the dorso-lateral margin for much of the abdominal region. Otherwise, the ventral tract has no definite boundaries. It merges with the following tracts and regions: (1) anteriorly with the capital tract; (2) dorso-laterally with the dorsal cervical region of the spinal tract; (3) more posteriorly and dorso-laterally with the antero-lateral termination of the interscapular region of the spinal tract; (4) at the level of the hindlimb it merges dorso-laterally with the femoral tract; (5) toward the tail it merges dorso-laterally with the postpelvic region of the spinal tract; (6) most posteriorly it merges caudally with the caudal tract.

*Ventral cervical region.*—Anteriorly the ventral cervical region merges with the capital tract; it merges laterally with the dorsal cervical region. In neither case is there a definite boundary. Posteriorly the ventral cervical region merges with the sternal region; here again the boundary is indefinite. The posterior three or four centimeters of the ventral cervical region is divided by the narrow anterior part of the midventral apterium.

*Sternal region.*—The sternal region merges anteriorly with the ventral cervical region. This junction is at about the level of the anterior limit of the lateral cervical apterium. The sternal region of each side is limited medially by the midventral apterium. Near its anterior end the sternal region gives off a narrow branch which extends dorsally and medially and merges with the anterior end of the scapulohumeral tract. Anterior to this branch the sternal region is limited dorsally by the ventro-lateral margin of the lateral cervical apterium. Posterior to the branch leading to the scapulohumeral

tract the sternal region is limited dorsally by the ventro-lateral margin of the lateral thoracic apterium. Toward the posterior end of the lateral thoracic apterium the sternal region gives off a large branch, the flank region. At the postero-ventral point of junction of the flank region with the sternal region the lateral thoracic apterium borders the dorsal limit of the sternal region. Finally, the sternal region toward its posterior limit merges dorsally with the femoral tract. The sternal tract merges caudally with the abdominal region. The posterior limit of the sternal region corresponds to the posterior margin of the underlying sternum.

*Flank region.*—The flank region diverges posteriorly and slightly dorsally from the dorsal margin of the sternal region. It overlies the knee and a small part of the tibiotarsus immediately distad of the knee. The flank region is bounded dorsally, posteriorly, and ventro-laterally by the lateral thoracic apterium. The lateral thoracic apterium has a narrow, hook-shaped extension which borders the flank region posteriorly and ventro-laterally. Nitzsch (1867) stated that the flank region is relatively inconspicuous in *Anseres* and that it is more pronounced in *Procellariiformes*.

*Abdominal region.*—The abdominal region merges anteriorly with the sternal region; posteriorly it merges with the postventral region. Medially the abdominal region of each side is bounded by the lateral margins of the narrow midventral apterium. Laterally and dorsally the abdominal region of each side is bordered by the ventro-lateral margin of the femoral apterium.

*Postventral region.*—The postventral region merges anteriorly with the abdominal region; dorso-laterally it merges with the postpelvic region. The right and left sides of the postventral region merge medially posterior to the anus and anterior to the under tail coverts. We consider the anal circlet a part of the postventral region. Anterior to the anus the right and left sides of the postventral region are separated by the midventral apterium.

#### FEMORAL TRACT

This tract lies on the upper part of the leg. It is bounded medially by the lateral pelvic apterium. Posteriorly the femoral tract merges with the lateral pelvic region; laterally it merges with the crural tract. The femoral tract is bounded anteriorly by the lateral thoracic apterium.

The acetabulum lies deep to the postero-lateral margin of the lateral pelvic apterium, and the femur extends antero-laterally from this point to the knee joint which lies deep to that part of the lateral thoracic apterium immediately medial to the posterior end of the flank region of the ventral tract.

The knee area and tibiotarsus immediately distad to the knee area are covered by the region of scutellation superficial to the distal end of the tibiotarsus.

#### CRURAL TRACT

This tract overlies the main muscle masses of the shank. The crural tract merges medially and ventrally with the posterior part of the sternal region. Anteriorly the tract is limited by the posterior margin of the lateral thoracic apterium. Dorsally and medially the crural tract merges with the femoral tract.

The knee area and tibiotarsus immediately distad to the knee area are covered by the flank region. The crural region extends over the remainder of the tibiotarsus to the region of scutellation superficial to the distal end of the tibiotarsus.

#### CAUDAL TRACT

Witherby *et al.* (1939) reported for the Mallard, "Tail rounded, 18 to 20 feathers, two central pairs (in some only one pair) curled, in eclipse straight." Phillips (1923) noted for the Mallard, "Four central tail feathers sharply upcurled and glossy black; rest of tail ashy colored with the margins of the feathers white." H. L. Clark (1918) reported on the number of rectrices and upper tail coverts in a number of genera of waterfowl. In *Anas* he found 16 rectrices and 18 upper coverts; however, we have been unable to confirm his results. In three specimens (two adults and one juvenile) of the Mallard we found 20 rectrices. Any recognition of a precise number of upper tail coverts must be made rather arbitrarily; there are at least as many upper tail coverts as rectrices.

Included in the caudal tract are the feathers of the uropygial gland and those located

laterally and posteriorly to that gland. The feathers anteriorly bordering the uropygial gland are included in the pelvic region. Humphrey and Butsch (1958) figured the distribution of the feather tufts around the two orifices of the uropygial gland in *Camptorhynchus labradorius*. In the Mallard there is a similar distribution in the form of a figure eight about the two orifices. Marked individual variations were found in the number of tufts surrounding these orifices in the Mallard; the respective numbers of such tufts in three specimens were 34, 30, and 27.

#### SUMMARY

The pterylosis of the Mallard (*Anas platyrhynchos*) is described, based on the examinations of fresh and preserved, clipped and unclipped specimens, and on soft-ray X-rays of the feather tracts of the trunk.

The carpal remex, diastataxy, and the reversed under wing coverts are discussed. It is noted that Steiner's hypothesis regarding diastataxy has been misinterpreted in the American literature.

The term POSTHUMERALS is used for the feather rows along the caudal margin of the skin covering the humerus. The group of feathers called by various authors the "scapular tract" or the "humeral tract" is here called the SCAPULOHUMERAL TRACT. The term FLANK REGION is given to that part of the ventral tract containing the flank feathers.

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## POPULATION MOVEMENTS OF BIRDS

By RICHARD F. JOHNSTON

This short paper is an exploratory discussion of three kinds of population movements of birds: dispersal, spacing, and migration. The last of these is of interest here only in its occurrence coincident with dispersal and spacing, and it is to the latter that chief attention is directed.

DISPERSAL refers only to movement, usually of young, from sites of birth to sites of breeding. "Effective distance of dispersal" refers to the least distance in an air line between site of birth and site (or sites) of subsequent breeding, and of course this is less in almost every instance than the distance actually traveled by an individual. The main significance of dispersal is ecological—by means of dispersal a species avails itself of suitable habitat within, peripheral to, or isolated from an occupied area. This general adaptation can be broken down into subcategories (Howard, 1960:157). There is, of course, important correlated function concerning movement of genetic elements through populations or between neighboring populations.

SPACING is the movement of birds that brings about territorial dispersion. Spacing is guided partly by configuration of their preferred vegetation and topography and partly by their territorial behavior. Territories of optimal quality tend to be occupied before those of suboptimal quality; consequently, a patchwork of occupied places can be established within a frame of generally suitable habitat. The routes that individuals follow in finding suitable places will reflect the fact that routes tend to be unknown beforehand, as are the locations of unoccupied places. Thus, the important elements of the environment in which spacing occurs are essentially distributed at random, as far as their influence on the direction and magnitude of spacing is concerned. For a population, therefore, spacing movements tend to cancel one another, that is, the vectorial sum of such movements approaches zero.

For a migratory bird, migration and dispersal (but not effective dispersal) more or less coincide in time. Additionally, terminal stages of migration and dispersal can merge with initial stages of spacing. Consequently, there is some reason for confounding these kinds of movement with one another; that we actually gain in distinguishing between them may be demonstrated in the following discussion.

## DISPERSAL

There is general agreement that the chief means of dispersal in birds consists of movements by young individuals. Almost forty years ago Grinnell (1922) recognized that individuals that moved long distances (so-called distributional accidentals) were predominantly young-of-the-year; extralimital occurrence was almost always of young birds. Fisher (1955) adduced further evidence showing that such movement, which he called dispersal, was a function of young, mainly first-year birds. Howard (1960) discussed this kind of movement by young individuals of several kinds of vertebrates. Most significant is the evidence from studies on banded, sedentary bird populations (Nice, 1937; Erickson, 1938; Kluijver, 1951; Gibb, 1954; Johnston, 1956), which has demonstrated movement from sites of birth by young-of-the-year and remarkable constancy of adults in remaining at sites of breeding.

In sedentary bird populations, but not necessarily in non-sedentary ones, the difference in amount of movement recorded for adults *versus* first-year birds is so great that a qualitative difference in behavior seems to be involved. Moreover, there are data supporting the idea that certain first-year birds characteristically move long distances in the process of dispersal. Table 1 presents a summary of distances moved in the dispersal

of Song Sparrows (*Melospiza melodia*) of two, distinct populations. Earlier (Johnston, *op. cit.*:42), the correspondence in distances moved in the two samples had been noted. Curves drawn from these data are bimodal and differ from curves characteristic of random dispersal mainly near the extremes of the frequency distributions. In both samples, more individuals move relatively short distances and relatively great distances than are expected to do so on the basis of chance alone. Therefore, dispersal can be considered to be an organized or directed characteristic in Song Sparrows.

TABLE 1  
DISTANCES OF DISPERSAL IN TWO POPULATIONS OF SONG SPARROWS

Population	Distance of dispersal in meters							
	100	200	300	400	500	600	700	800+
California <sup>1</sup>	39 <sup>2</sup>	30	12	8	0	0	8	3
Ohio <sup>2</sup>	12	27	30	8	6	8	3	6

<sup>1</sup> From Johnston, 1956:42.

<sup>2</sup> From Nice, 1937:83.

<sup>3</sup> Per cent of total instances.

Studies on other kinds of sedentary animals have shown their dispersal qualitatively to resemble that of Song Sparrows. Bateman (1950) noted several examples of bimodal curves in the dispersal of flying insects in his analysis of "dispersal" of genes in populations. He concluded that "many if not most methods of gene dispersal produce such distributions," although he had no examples from terrestrial vertebrates at that time and he did not limit his conclusion to strictly sedentary populations. Bimodal curves of dispersal have been demonstrated for a leafhopper, *Macrosteles divinus* (Frampton, Linn, and Hansing, 1942), a weevil, *Bruchus pisorum* (Wakeland, 1934), a lizard, *Sceloporus olivaceus* (Blair, 1960), the House Finch, *Carpodacus mexicanus* (Thompson, 1960), the House Sparrow, *Passer domesticus* (Wagner, 1959), and a mouse, *Peromyscus maniculatus* (Dice and Howard, 1951). All available evidence indicates that such bimodal distributions are reflections of species-specific behavioral tendencies in dispersal; the preponderant fraction of the dispersing element is characterized by movement of relatively short distance (the "homing tendency" of Howard, *op. cit.*), and the lesser fraction of the dispersing element by movement of relatively long distance.

Thus, the tendency by subadults to move is evident in any fraction of this age class. Were there actually no tendency to move on the part of some individuals, the curves of dispersal would show a greater frequency of individuals staying at birth sites. Yet, few occur exactly at birth sites, and modal distances of dispersal for Song Sparrows, one of the most sedentary of bird species, are 200 to 400 meters. If it is necessary to emphasize one thing in order to establish dispersal as an innate tendency, the emphasis is properly placed on those young having the capacity to disperse long distances. Howard's review (*op. cit.*) has led him to a similar conclusion.

It is appropriate to note at this point that the genetic background for dispersal is complex. That only a small fraction of young disperse long distances is of adaptive significance. Also, there are different selective values for long-distance (or short-distance) dispersal in accord with whether the phenotype is present in centrally-located populations or at the periphery of the distribution of the species. Such fluctuating selective value on phenotypes (which may be composed of several genotypes) can, as Alden H. Miller has noted (personal communication), result in behavioral polymorphism. In such an instance, central populations would show a greater, and peripheral populations a lesser,

incidence of phenotypes dispersing long distances—conditions that could be demonstrated by appropriate intensive population studies.

#### SPACING

The fact that young individuals are the agents of dispersal provides one measure of the distinction between dispersal and spacing. Additionally, spacing, motivated in part by territorial behavior, results in the dispersion of breeding units in a population, and it would seem, to consider only two alternatives, that territorial aggression, rather than spacing itself, is the significant selective element in territorial behavior. It would also appear that spacing is not immediately related to dispersal.

Nevertheless, territorial spacing and dispersal have been associated causally (Fisher, 1955:440; Howard, 1960:152). The suggestions were that dispersal ("environmental dispersal" of Howard, *loc. cit.*) in sedentary (*ortstreuen*) bird species is attributable to the "territorial system." These suggestions were probably motivated by undue emphasis on the significance of territoriality. A tremendous amount of work in the past two decades and especially a paper by Pitelka (1959:253) serve clearly to point up the general conclusion that spacing of individuals or breeding units is the immediate adaptive advantage of territoriality; behavioral systems of territoriality result in ecologic systems of spacing. Indeed, the 31 functional categories listed by Carpenter (1958) chiefly have as their common denominator the phenomenon of spacing.

Territoriality in the northern hemisphere is a phenomenon chiefly of spring and summer; yet, by early spring (or autumn and winter for some species) dispersal has already been achieved. This is true almost without exception for sedentary, resident birds (Johnston, 1956:40), but it is less true for migratory species. In the latter, dispersal and migratory movement are identical, as has been noted previously; dispersal is thus nearly complete only when migration ceases. However, spacing functionally equivalent to dispersal occurs in early stages of territorial behavior. Effective distances of dispersal can consequently be increased or decreased depending on chance encounters of non-established birds with established birds. Such modification is the chief bearing of territorially-activated spacing movement on dispersal, and it should be clear that such bearing means little. The essential meaninglessness is emphasized particularly at the level of populations, in which as many individuals will be forced to move one way as another. In sedentary populations showing autumnal territoriality, the action of territorial aggression on juveniles that are dispersing would be evident in autumn, not spring, but the significance of territoriality in affecting meaningful modification of dispersal would be the same as that discussed for migratory species.

The term spacing is available and suitable for discussing movement resulting from territorial behavior, and it is here proposed that it be used as distinct from dispersal.

#### CONCLUSIONS

Dispersal, defined as movement from site of birth to site of breeding, is a mechanism that tends to ensure complete testing or investigation by a species of all suitable habitat within and beyond the area of established distribution of this species. This fragment of the population that disperses is the young; in birds such individuals are usually less than one year old. The genetic heritage of some of the individuals probably casts them in the roles of dispersers to long distances.

Spacing, resulting from territorial behavior of adults and responsible for dispersion of breeding units, does not effect, or in any meaningful way affect, dispersal. The capacities for these two types of movement exist independently of one another, in spite of the fact that some dispersal can occur coincident with spacing.

Migratory movement includes dispersal *in sensu lato*, but effective dispersal is independent of migration.

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## THE BREEDING CYCLE OF THE YELLOW-BELLIED SEEDEATER IN PANAMA

BY CORA C. ALDERTON

This report on the Yellow-bellied Seedeater (*Sporophila nigricollis*) is part of a five-year study of the life histories of some common tropical birds of the Panamá Canal Zone. The species is widely distributed in the tropics and occurs in a variety of habitats over a great range of altitude. On the Isthmus of Panamá, it is a "common open-country species" (Eisenmann, Smiths. Misc. Coll., 117, no. 5, 1952:58). Sturgis (Field Book of Birds of the Panama Canal Zone, 1928:394), using the former name *S. gutturalis*, states that it is present in the Canal Zone "chiefly in the rainy season." Wetmore (Smiths. Misc. Coll., 102, no. 2, 1952) notes that the "distribution of the species in Panamá is not clearly understood at present and seems in part to be seasonal as the birds are reported to appear during the rains in localities where they are absent during the dry season."

The author watched these seedeaters closely in 1956, 1957, and 1959. In these years, a pair nested so near the house that they could be seen from inside the house or from the breezeway below. Occasional observations were made on other pairs. A total of eight pairs and nine nests was watched. The males of 1956, 1957, and 1959 were different individuals, as indicated by plumage characters.

In 1956, one pair built three nests. Although all of the nests were unsuccessful, nest building was watched for 25 hours and singing behavior was followed for a period of 20 days. In 1957, the female disappeared midway through the nestling period and the male carried on until the nest was vacated. In 1958, one nest was checked for length of the incubation and nestling periods. In 1959, a nesting pair was checked occasionally from July 31 to August 15 and from September 7 to 26. The nest of this pair was watched for nearly 87 hours from September 27 to October 9 from inside the house, some 15 feet away.

### THE STUDY AREA

The area in which these seedeaters were observed is situated in South Gamboa, Panamá Canal Zone. It is south of the Chagres River near the point where the river flows into the Canal. The elevation is 110 feet; the vegetational cover is tropical deciduous forest.

The year at this locality can be divided into two seasons: the dry season which extends from mid-December to mid-April and the wet season which occurs during the remaining eight months. Relative humidity varies greatly between the two seasons, the averages being in the middle seventies and the high eighties, respectively. The average rainfall from 1955 to 1959 varied only from 87.55 to 87.17 inches. Monthly variation for these years ranged from no precipitation in March, 1957, to 17.4 inches in October, 1959. These meteorological data were supplied by the Meteorological and Hydrographic Branch of the Panamá Canal Company.

### LENGTH OF THE BREEDING SEASON

Table 1 presents the dates for the first and last local appearances of Yellow-bellied Seedeaters, the length of their stay, and the dates of first songs in the study area, for the years 1956 through 1959. Since these birds are silent on arrival, some leeway should be granted for the dates of first arrival and the tabulation should be regarded as approximate.

In 1956, the site of the first nest was selected on June 20, 79 days after the arrival of the first male. This nest was complete 18 days later, on July 8. In 1957, the long drought which had started in December, 1956, was not broken until May 11. In May, the gauge at Gamboa, about one mile from the study area, registered 1.74 inches of rainfall above average. The Yellow-bellied Seedeaters arrived almost a month later. Their early departure on October 14 made this the shortest of the four seasons. In 1958, the Gamboa station recorded subnormal rainfall in every month except January and May. The accumulated deficit for the year was 17.57 inches. The birds arrived on

TABLE 1  
LENGTH OF BREEDING SEASON

Year	First appearance	Last appearance	Number of days	First songs
1956	April 3	October 28	209	May 23
1957	June 8	October 14	128	—
1958	April 25	December 14	224	May 9
1959	April 7	October 18	195	May 14

April 25; rainfall in May was 2.3 inches above average and the first song was heard on May 9. As late as December 7, a pair of adults was feeding a juvenile in a small flock of seedeaters beside the Panamá Railroad at the Gamboa end of the bridge over the Chagres River. Twelve individuals were present in this flock; they disappeared on December 14. In 1959, the first individual was seen on April 7. The preceding year had ended with a rainfall deficit, and the first four months of 1959 were all below average. Even so, there was enough moisture for growth of the grass and other vegetation on which this species depends. The rainfall in May was 2.13 inches above average. The first song was heard on May 14.

The fluctuating amount of rainfall over the more than 70 years for which there are records has apparently not produced conditions of drought over periods long enough to change the nature of the vegetation on which these seedeaters depend. Each year the new crop of food plants grows in time to assure food throughout the nesting season. Further attention should be given to the relation of the food supply to the length of the breeding season. The presence of a juvenile still being fed as late as December 7, 1958, points to the need for more data.

#### TERRITORY

Territory is quickly established and territorial boundaries can be defined by the location of song perches. Boundaries are defended by aggressive behavior ranging from soft warning calls to furious attacks. Perches used for territorial advertising were much the same in 1956 and 1957. Those most frequently used were telephone, power or clothes lines, and trees of several kinds, including broad-leaved species and palms. In both seasons, the Yellow-bellied Seedeaters shared the perches of the Blue-black Grassquits (*Volatinia jacarina*) on three inflorescence stems of a palm. When the last stem fell, the grassquits quickly adjusted to the new location on the ground, whereas a Yellow-belly was seen to use it only once as a perch.

Because of the great amount of suitable terrain in the study area, territories were established without conflict from 1955 through 1958. In 1959, three males attempted to establish territories in the study area. The only conflict noted was between August 10 and 14 of that year, when a male tried to settle in an occupied territory. After four days, the intruder finally left, leaving the original pair in full possession.

Yellow-bellied Seed eaters are not particularly aggressive in defense of territory. Only when another bird came near the nest did the pair show marked belligerence. The male, or the female, or both together, would rush the intruder and drive it away. There was a tendency for the male to advertise territory while the female attacked the trespasser. The male tended to be concerned with the entire territory while the female was concerned with the nest proper. In territorial disputes, aggressive displays often were effective without physical contact. Second nests are usually located within the territory in which the first nest is built. After the nestlings of the first brood have been fledged, territorial defense is relaxed temporarily and resumed when the new nest is under construction. Territories are abandoned after the last fledgling of the last nest has been safely hidden at considerable distance, or when conditions of weather and climate bring the breeding season to an end.

#### VOICE

The male Yellow-belly's song is a single, unpunctuated phrase ending in a short trill, the last one to three notes of which are slurred. When disturbed, a male may abruptly break off singing in mid-phrase, leaving the song incomplete. During pauses between songs, males frequently preen.

The male has a variety of other vocalizations. While weaving the nest, he makes rapid, chattering sounds in a low monotone. He recognizes the arrival of the female with a single note repeated a few times and occasionally followed by a song. Short, low, nasal notes uttered in rapid succession—a sort of purring—may be used while approaching the nest, or from the interior of the nest during construction. A low *hist* is interspersed with *chee* notes when a male, on the alert, watches the nest from nearby. The alarm notes are single, given in a rapid series in a high, harsh tone.

The female does not sing. On arrival at the nest during the incubation period she usually gives a trill to which the male replies with a single note. No listener could mistake the purpose of her harsh, scolding notes when she drives an intruder away from the nest. When chased, her flight is accompanied by sharp, high-pitched notes. When weaving, she makes soft *chip-chip* sounds and also gives a high-pitched, chattered trill followed by single, sharp notes. Repeatedly, the end of her flight to the nest while building is accompanied by a series of rapid, descending notes.

The most frequent use of the male's song was for territorial advertising, but it may also have helped to maintain the pair bond. When the male fed the young, he often preceded or followed each feeding with a song. Singing began before nest building and continued until well after the young had fledged. In 1957, after his second mate had apparently lost interest in nest building, the male continued to sing vigorously for many days. This male roosted at the extremity of his territory east of the house. His first and longest song period began at dawn. Depending on the amount of light present, the time of beginning his dawn song varied as much as 15 minutes. If it was raining heavily, dawn singing was omitted. After his dawn song, the male regularly came near the nest and sang while the female was still sitting. He remained within sight of the nest and sang from several perches while his mate took her first, and usually longest, recess. In 1956, July 8 was the last day of nest building and the day before the first egg was laid. The male began this day with vigorous singing, moving from perch to perch. In 46 minutes, from 5:54 to 6:40 a.m., he sang 233 times, singing from one to 23 times on different perches. At other times of the day he moved from one song perch to another, preening between songs and occasionally feeding briefly on green seeds of Guinea grass. Song periods at one perch usually lasted about eight minutes, occasionally as long as 15 to 18; from one to 100 songs were given from a single perch.



## THE NEST AND NEST BUILDING

The nest tapers slightly to a blunt cone which fits into the crotch formed by three or four twigs in a small tree or shrub; the cup is round and shallow. Invariably clusters of leaves conceal the nest from above, although it may be seen from the side or below. The materials used are brown, dry grass stems with some rather stiff fibers, such as those in the sheath at the base of a date palm leaf. The outside wall, so thin that the nestlings can be seen in silhouette through it, affords good ventilation.

Each member of the pair takes part in building. The male takes the initiative and does most of the work for a few days. The female then takes over and completes the nest; the male accompanies her when she goes after materials but does no more weaving. The supporting twigs are first wrapped with gossamer. Although these fine filaments are invisible to the observer, each member of the pair has been seen at the nest site making the motions of attaching something to a twig and then stretching its head around to the opposite side of a stem to complete the fastening. Eight days of such work were put in by one pair before any signs of construction could be seen from a distance of 15 feet. Several days more are required to make the hammock-like foundation. The nest wall is then completed and topped by a slight but firm rim which is used for landing and takeoff. The completed structure withstands successfully torrential rains and high winds. The first nest of 1958 took 18 or 19 days to build.

When the first nest is empty, the pair starts a second nest, using the materials from the first. Second nests require less time for construction, in part, perhaps, because of the availability of materials from the first nest, and in part because of the demands of the advancing season.

Six of nine nests built in three seasons were measured. All but one had inside diameters of 2 inches by  $1\frac{3}{4}$  or  $2\frac{1}{2}$  inches. The sixth nest measured  $2\frac{1}{2}$  by  $2\frac{3}{4}$  inches. Five nests were about 10 feet above the ground; the others were 5.3, 6.0, 7.7, and 9.5 feet up.

All but two nests were placed in hibiscus shrubs; of the other two, one was on a branch of a lime tree and the other near the top of a croton. Six nests were placed in a hibiscus hedge. In 1959, this hedge had been cut back to less than four feet in height. Although the male frequently sang from a shrub in the hedge, the pair located its nest in a croton which was about 11 feet high, only 12 feet from the hibiscus hedge.

The behavior of three pairs suggests that the male selects the site for the nest and that the female, after much exploring, both alone and accompanied by the male, finally settles on the site originally selected by the male. This is illustrated by the behavior of the unfortunate pair watched in 1956. After two nests had been built and the eggs in each had been destroyed by snakes, the female apparently wanted to build the third nest in a mango tree outside the limits of the territory. For several days she industriously carried materials to a spot in the tree much higher than any in which a nest had been located. The male accompanied her on these trips but did not give up his territory. In the end, the third nest was located in the eastern section of the same hibiscus hedge in which the first two had been built.

## THE EGGS AND INCUBATION

The eggs are ellipsoid and very dark. They are greenish white in color mottled thickly with brown to purplish blotches which are slightly more concentrated at the larger end. There were no noticeable differences in size or color among clutches laid by various females in different seasons. In every case the complete set contained two eggs. On August 16, 1955, a female was seen to eat the shell of a newly hatched egg. Whether or not the male also eats the eggshells was not observed.

Data on incubation are mainly from the nests of 1957 and 1958. Only the female

incubates. The first nest of 1957 contained two eggs, both of which hatched. The incubation period for the second egg was 12 days, from August 25, between 7:55 and 8:25 a.m., to September 6, shortly before 8:29 a.m. In 1958, the first egg was laid early on July 7 and the second on the morning of July 8. On July 19, at 2:20 p.m., both eggs were intact. On July 20, at 12:30 p.m., two nestlings were present, one obviously a few hours older than the other. The incubation period appeared to be about 12 days. In 1959, two eggs were laid on September 16 and 17, respectively. Incubation probably began late on September 17 and it was definitely under way on September 18. On September 28, there appeared to be one egg and one nestling visible through the bottom of the nest. At 8:41 a.m. on September 29, the male put his head into the nest. When he raised his head he was working his bill, possibly eating eggshell or a fecal sac. On the basis of his behavior, it seems likely that the second egg hatched prior to 8:41 a.m., September 29, and had an incubation period of 11 or 12 days.

For the nest watched in 1957, the average of 108 diurnal sessions of attendance (S) was 21.8 minutes. The average of 106 recesses (R) was 7.6 minutes. The sessions ranged from 2 to 67 minutes. The longest session recorded was 87 minutes on July 22, 1956. Recesses ranged from 1 to 24 minutes. Using Skutch's (Pac. Coast Avif. No. 31, 1954:15) formula for computing the percentage of time (T) spent on the nest,  $T = S \div (S + R) \times 100$ , attendance at the nest was 74.1 per cent.

Six pairs of seedeaters were watched from 1955 to 1959. They produced a total of 16 eggs of which ten hatched; of the ten young, six were fledged. Expressed in percentages of the total number of eggs laid, 62.5 per cent hatched and 37.5 per cent of the young were fledged. Of the ten eggs that hatched, 60 per cent of the young were fledged, including two young that were force-fledged in 1959. The known losses were the result of predation by tree-climbing snakes.

While sitting, the female changes position frequently, rakes in the nest with her feet, and pokes the nest wall with her bill from a sitting position. Very frequently she goes below the nest and works at the outside. Just what she accomplishes could not be determined but this behavior was characteristic of females watched in 1956, 1957, and 1959. The males pay close attention to the nest and visit it several times soon after the first egg has been laid. They may spend as much as four minutes peering at the egg from different angles.

From time to time, the members of the pair communicate with each other. On September 5, 1957, the last day of incubation, the male began his dawn songs at 5:37 a.m. in the jungle in which he roosted. He sang until 5:55 and then came near the nest and sang a few more times. His mate was still sitting and did not leave until 6:13 a.m. Thereupon the male sang four times, paused, and sang five times. The female returned at 6:20. The male sang twice at 6:24 and the female answered with a laconic *chip*. The male then moved and sang 15 times, paused, then sang four times. After a silence of 12 minutes he moved near the nest and sang 21 times. At 6:49 the female repeated her single *chip* 21 times until the male sang at 6:53 a.m. At 7:25 she gave her chitter and left the nest. As usual, the male sang when she left. The female returned at 8:14 a.m.

The complete record of incubation would include night sessions spent on the nest by the female. In 1959, her retiring time depended on the amount of light present but occurred sometime between 5:00 and 6:00 p.m. The female left the nest in the early dawn; her earliest departure was at 5:59 a.m. and her latest at 6:13 a.m. Her night sessions on the nest thus averaged about 12 hours.

#### THE NESTLINGS

*The nestling period.*—Of nine nests found in five consecutive seasons, only two pro-

vided data on the length of the nestling period. In 1957, the second nestling was fledged at eight days; in 1958, the second nestling was fledged at nine days; in 1959, the nestlings were force-fledged.

**Brooding.**—Only the female brooded the young. In 1957 during the first three days following hatching, the female invariably brooded after she had fed the young. This routine was followed until 11:26 a.m. on the fourth day and until 9:00 a.m. on the fifth day. Observations on each day were discontinued at 12:05 p.m. The female spent the night on the nest as she did in the incubation period.

The duration of brooding did not appear to be correlated with air temperature. Sometimes the young were brooded when the temperature was high and at other times they were left uncovered when air temperatures were lower. Although the nestlings were left uncovered when air temperatures were from 20° to 40° F. lower than the probable body temperatures of the adults, they did not seem to suffer. The location of the nest, under an umbrella of leaves which provided partial protection from the direct rays of the sun and from the worst battering of the rain, undoubtedly helped the young to survive. In 1957, the female of the first nest disappeared when the young were five days old, but the male continued to sleep on his perch as before. Although the young undoubtedly felt the cold during the night, they survived to fledging.

TABLE 2  
FEEDING RATE BY SEX OF PAIR OF YELLOW-BELLIED SEEDEATERS IN 1957

Date	Observation period in minutes	Male		Female		Total feedings	Notes
		Number of meals brought	Number per hour	Number of meals brought	Number per hour		
Sept. 6	120	2	1.0	2	1.0	4	Two nestlings hatched early; each was fed approximately twice in the 2 hours
7	308	7	1.3	14	2.7	21	Workmen near house—very noisy
8	210	8	2.3	11	3.1	19	1:10 p.m. to 4:40 p.m.
9	358	18	3.0	18	3.0	36	Both a.m. and p.m. tallies
10	273	17	3.7	19	4.1	36	Last day with both parents
11	457	31	4.1	....	....	31	Male alone with two nestlings
12	667	106	9.5	....	....	106	Same
13	510	37	4.3	....	....	37	One nestling; probably also one fledgling
14	107	9	5.1	....	....	....	Not representative; nest vacated before 11:30 a.m.

**Feeding.**—Both parents feed the young. Food is usually regurgitated, although some food is carried to the young in the bill. When feeding the young, the parents, in turn, poked from one gaping throat to the other in a fast and regular rhythm. The nearer a chick was to a parent, the more feedings it received. In the first four days of the nestling period in 1957, the older nestling used its sibling as a "pillow"; thus it was in position to receive food several times before the other had raised himself to feeding position. Sometimes the female, in subsequent feedings, compensated for this disparity, but the male never did. Fecal sacs were eaten by both parents during the first few days but later were carried considerable distances and dropped.

Data on feeding at the nests of 1957 and 1959 are given in tables 2 and 3. It is difficult to compare the data since the female of 1957 was present for only five days and, further, the exact hatching time in 1959 was not certainly known, so that the first day

recorded in table 3 may not be the first day on which the young were fed. Nevertheless, it is apparent that the females at both nests fed more often than their mates and that the female in 1959 made fairly consistent gains in feeding rate, reaching her maximum rate on the next-to-last day of the nestling period. The record of the male of 1959 is even more consistent, culminating in a maximum feeding rate on the last day of the nestling period. At this particular nest, the behavior of the parents was consistent with the increasing demands of the growing young. The feeding rates of the two males are comparable save for September 12, 1957, when the male more than doubled his feeding rate over that of the preceding day. This is explained in the following section.

#### BEHAVIOR OF THE MALE AFTER LOSS OF MATE

When the female of the pair watched in 1957 disappeared, it seemed questionable that the male could provide for the needs of his half-grown nestlings. On September 11, his first day alone, the nestlings were in their sixth day. After his dawn songs the male visited several perches and advertised territory before going to the nest. Between 7:20 and 8:10 a.m., he gave the young five meals. This was quite as usual. Between 8:45 and 9:45 there were no feedings. In this period, the male was first disturbed by an iguana that ate a hibiscus flower directly over the nest. After the iguana departed, a

TABLE 3  
FEEDING RATE BY SEX OF PAIR OF YELLOW-BELLIED SEEDEATERS IN 1959

Date	Observation period in minutes	Male		Female		Total feedings
		Number of meals brought	Number per hour	Number of meals brought	Number per hour	
Sept. 30	470	15	1.9	14	1.8	29
Oct. 1	368	15	2.4	23	3.7	38
2	500	27	3.2	26	3.1	53
3	480	30	3.7	28	3.5	58
4	592	32	3.2	43	4.3	75
5	631	43	4.0	51	4.8	94
6	590	43	4.3	46	4.6	89
7	422	33	4.7	49	6.9	82
8	560	52	5.6	45	4.8	97
Totals		290		325		615

Rufous-tailed Hummingbird (*Amazilia tzacatl*) darted about the nest shrub and flew up and down the length of the hedge in which the nest was located. The male moved about through the bushes, alert, but he did not leave the area despite the begging of the nestlings. Between 10:18 a.m. and 12:25 p.m., he fed the young eight times. Observations were resumed at 2:30 p.m., but he brought no food to the nest until 3:00; from then until 5:37 he fed the young 18 times. His feeding rate for the entire 7 hours and 37 minutes of observation was 4.1 trips to the nest per hour, but in the last two hours and 37 minutes of observation he fed at the rate of 6.9 trips per hour, an indication of the speed which he had worked up in the latter part of the day. On September 12, the male fed the nestlings 106 times in 11 hours and 7 minutes and achieved his highest feeding rate of 9.5 trips per hour. On September 13, only one nestling was present when observations were begun at 7:30 a.m. This nestling was not fed until 9:02, although the male had come once to inspect the nest. The feeding rate of the male for the eight and one-half hours of observations was 4.3 trips per hour, almost the same as the feeding rate noted on September 11. Whether the male was devoting all his time to

the one remaining nestling or dividing his time between it and a fledgling could not be ascertained.

The singing rates of the males of 1957 and 1959, exclusive of dawn song, are compared in table 4. The great decrease in the hourly singing rate of the male of 1957 after his mate disappeared is quite evident. On his first day alone, September 11, almost all of his singing was done in the morning; between 2:30 and 6:00 p.m. only one song was heard. On September 12, exclusive of dawn singing, no song was heard. As his feeding rate picked up, his singing rate decreased sharply. On September 13, when only one nestling remained, with, perhaps, a fledgling outside the nest, his singing rate started to pick up again. The male observed in 1959 tended to increase his singing rate toward the end of the nestling period, even though his feeding rate was also increasing. If the performance of this male was normal, then it is obvious that the singing rate of the male of 1957 was greatly influenced by the disappearance of his mate and his having to carry on alone after September 11.

*The second mate, 1957.*—On September 13, when the lone male was still feeding one nestling, a young female Yellow-belly perched on the clothesline, gave two *cheep* notes,

TABLE 4  
RATES OF SINGING AND FEEDING BY MALE YELLOW-BELLIED SEEDEATERS IN 1957 AND 1959

Male, 1957				Male, 1959			
Date	Feedings per hour	Songs per hour	Notes	Date	Feedings per hour	Songs per hour	Notes
Sept. 7	1.3	....	Songs not tallied	Sept. 30	1.9	....	Songs not tallied, but frequent
8	2.3	28.8	Both parents	Oct. 1	2.4	....	Same as above
9	3.0	44.5	Both parents	2	3.2	46.4	Both parents from beginning to Oct. 9
10	3.7	25.2	Both parents	3	3.7	45+	
11	4.1	6.0	Male alone; two nestlings	4	3.2	49.0	
12	9.5	0	Same as above	5	4.0	65.7	
13	4.3	5.5	One nestling	6	4.3	46.4	
14	....	....	Nest vacated before 11:30 a.m., workmen near nest	7	4.7	148.9	
				8	5.6	88.3	
				9	....	....	Nestlings forced from nest by Southern House Wren

and preened; she was soon joined by another female. The male moved to a perch about 18 inches from the nest, and the two visitors perched beside him. One of them scolded and both flew away but they soon returned, one to the male's perch. He chased them away but they did not go far and one returned to perch directly above the nest. The male scolded, and when the female started toward the nest he drove her away. Again she used his perch, but briefly. In quick succession he sang seven times from as many perches and was answered each time by a Yellow-belly in the area south of the lane. For a time he continued to feed the nestling without interference, but at 11:15 a.m. the intruding female again came to his perch, then she moved to the nest and picked at the bottom. Moving around it she picked up a fiber which she held for some time. Again she perched beside him and again he drove her away and fed the nestling.

It rained from 11:22 a.m. to 12:45 p.m., but the male, looking bedraggled, fed

the nestling. In one 12-minute period he sang a few times and was again answered by a male to the south. At 1:45, a female, possibly the same one seen before, perched on the top stem above the nest, then on the male's look-out perch. He scolded and threatened her and she moved away but promptly returned to the nest while he watched her. She flew away for a moment and he fed the nestling again. When she returned and began to pick at the nest he drove her away, sang once, and followed her out of sight. She was not seen again that day, and the male continued to feed the nestling at intervals of about five minutes.

This female was very persistent and obviously ready to nest. It seems likely that she was the second mate with whom he soon built a nest in another section of the same hedge, although it was not possible to determine this on the basis of individual identification. The first nest was vacated on September 14. On September 17, the male's singing rate had risen to 94.8 songs per hour, and on September 23 he sang 201 songs in one hour. The new nest was started between September 17 and 23. The only egg was laid on September 28 and was lost on October 10. If the second mate was indeed the female that stayed so persistently near the nest on September 13, and had picked at it several times, it is of interest that she made no attempt to feed the lone nestling present. This may have been an indication that she was in an early stage of the reproductive cycle, ready to build, but not yet ready to feed young. The male, on the other hand, although he had lost his mate, defended the nest against the intruding female and continued to feed his young.

#### SUMMARY

The Yellow-bellied Seedeater (*Sporophila nigricollis*) at South Gamboa, Panamá Canal Zone, was seen during the rainy season only, when the vegetation on which these birds depend for food is present.

Territory is established quickly. The male tends to defend the entire territory, whereas the female tends to defend the nest only.

The nest is built by both members of the pair. The male takes the initiative and does most of the work for a few days; the female then takes over and completes the nest. One nest took 18 or 19 days to build.

Complete clutches invariably contain two eggs. Only the female incubates; she spends about 74 per cent of her time on the nest.

The nestling period is eight or nine days. Only the female broods, but both sexes feed the young.

*North Miami Beach, Florida, January 24, 1961.*

## BIRDS FROM THE MIOCENE OF SHARKTOOTH HILL, CALIFORNIA

By LOYE MILLER

For nearly half a century a small eminence just north of the Kern River, where it emerges from the mountains in Kern County, California, has borne the local name of Sharktooth Hill. Unrecorded thousands of beautifully preserved shark teeth have been taken from the loose sands along its eroded flanks. Whales, sea lions and several species of maritime birds have likewise been recovered from the deposit that is assigned to the Temblor phase of Upper Middle Miocene age. Mr. Edward Mitchell of the University of California, during a search for mammalian remains, retrieved a small number of bird bones which he most generously presented to me. They constitute the basis for this study.

## ACKNOWLEDGMENTS

My sincere thanks are extended to Mr. Mitchell for his gift. Further indebtedness is acknowledged to Dr. G. Dallas Hanna of the California Academy of Sciences and to Dr. R. A. Stirton, Museum of Paleontology, University of California, for the loan of type specimens of previously described species from the deposit. Appreciation is expressed to Dr. Alden H. Miller and Mr. Gene M. Christman of the Museum of Vertebrate Zoology for advice, facilities and photography, in addition to many personal courtesies.

Technical descriptions of bird material from the area were first published by Wetmore (Proc. Calif. Acad. Sci., 19, no. 8, 1930:35-93), who recorded a shearwater, a gannet and a gigantic goose. Since then, nothing has come to my attention that deals with the avifauna of the locality.

## MATRIX

The fossil-bearing stratum consists of a fine gray sand of fairly uniform texture that crumbles easily in the fingers, and the shark teeth along with the smaller bones are generally obtained by passing the crumbled material through coarse sieves.

Unlike the beautifully preserved skeletons from the Lompoc Miocene (Miller, Carnegie Inst. Wash. Publ. 349, 1925:109-117), the bird remains are fragmented and are totally unassociated. Petrification, however, is complete and there is very little corrosion except in the case of *Morus vagabundus*.

Marine mammals, however, are represented by some articulated skeletons which fact would indicate deposition of the formation under relatively calm water.

## THE BIRD FAUNA

## PROCELLARIIFORMES

*Puffinus inceptor* Wetmore (*op. cit.*) was described from a distal fragment of the humerus in the collections of the California Academy of Sciences as the first bird known from the Sharktooth Hill quarry. He mentions a second imperfect specimen of *Puffinus*, also, but does not allocate it to species. This paper describes two new species of the genus.

*Puffinus priscus* new species

*Type*.—No. 58185, Mus. Paleo., Univ. Calif., Berkeley; the distal third of a left humerus.

*Locality and age*.—From locality V-2401, Sharktooth Hill, Temblor Formation, Upper Middle Miocene.

*Diagnosis*.—The specimen differs from *P. inceptor* Wetmore (1) in having a thinner, flatter shaft; (2) in having a longer, more slender ectepicondylar process, that is, less triangular; (3) this process

is set closer to the radial condyle and the condyle overhangs it more sharply; (4) the radial condyle is relatively larger and is prolonged farther toward the median line of the shaft; (5) the ulnar condyle is smaller and the entepicondyle is less extended distally; (6) the intercondylar furrow is far less open; (7) the brachial depression is narrower and is less extended up the shaft (proximally); (8) the attachment of the anterior articular ligament is broader and higher.

The specific name signifies "that which has passed away."

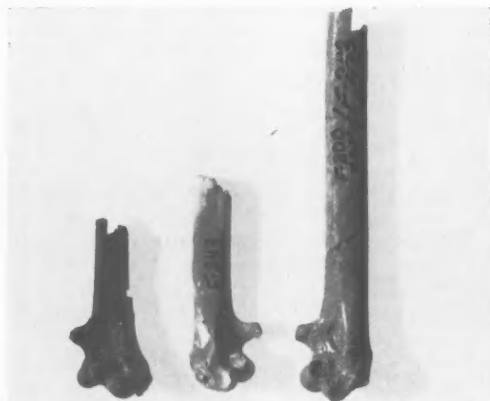


Fig. 1. Type specimens of *Puffinus inceptor* (left), *Puffinus priscus* (center), and *Puffinus mitchelli* (right) from the Miocene of Sharktooth Hill, Kern County, California. All figures are natural size.

***Puffinus mitchelli* new species**

*Type*.—No. 58184, Mus. Paleo., Univ. Calif., Berkeley; the distal half of a right humerus.

*Locality and age*.—From locality V-2401, Sharktooth Hill, Temblor Formation, Upper Middle Miocene.

*Diagnosis*.—The specimen differs from *P. inceptor* (1) in being much more robust; (2) the intercondylar furrow is much less open; (3) the ectepicondylar process is less developed; (4) the attachment of the anterior articular ligament is more strongly developed; (5) the ulnar condyle is less extended beyond the radial condyle, which would seem to set the axis of flexure at the elbow more nearly at right angles to the general line of the humerus; (6) the ectepicondylar process is less triangular in shape; (7) the brachial depression is less extended up the shaft; (8) the shaft is broader and thicker; (9) the shaft narrows down less rapidly in passing proximally from the region of the condyles.

The species is named in honor of Edward D. Mitchell, the collector, who shows great promise in paleontology.

*Remarks*.—The great width of the intercondylar furrow in *P. inceptor* gives the impression (see table 1) that the bone is larger than it really is. With the three fossils in hand, it is seen to be intermediate in size between *P. priscus* and *P. mitchelli*.

The more distal position of the ulnar condyle, together with this open intercondylar furrow, sets the species *inceptor* aside from all other species of shearwater, fossil or Recent, that I have been able to examine. Were it a bird in full flesh and plumage today, it would doubtless be assigned to a separate subgenus at least.

Such an assembling of several congeneric species in one locality is not really out of order. In many years of patrolling the Los Angeles County beaches, I have retrieved four species of shearwaters that had been cast up by the sea.



The present study indicates that there were at least three species of shearwater (*Puffinus*) in the Sharktooth Hill area at the time of deposition. Wetmore (*op. cit.*) described *Puffinus inceptor* and recorded an unspecified fragment of the same genus which may or may not be assignable to one of the species described above. All three seem to have been larger birds than *P. diatomacus* known from the Lompoc shales, which are of the same age, but lie on the open Pacific side of the Coast Range barrier to the west, and from the Lomita shales of southern California.

TABLE 1

MEASUREMENTS IN MILLIMETERS OF THE DISTAL END OF THE HUMERUS IN *Puffinus*

	Miocene — Sharktooth Hill			Recent — California	
	<i>P. inceptor</i>	<i>P. priscus</i>	<i>P. mitchelli</i>	<i>P. griseus</i>	<i>P. opisthomelas</i>
Breadth through condyles	10.0	7.5	8.5	9.5	7.5
Width through shaft	6.0	6.3	7.0	8.0	5.7
Thickness of shaft	3.5	3.5	4.2	4.3	3.0

## PELECANIFORMES

*Morus vagabundus* Wetmore

The type specimen of this species is the extreme distal end of the right humerus said by Wetmore (*op. cit.*) to be "similar to *Morus serrator* but decidedly smaller." A proximal fragment of the humerus collected by Mr. Mitchell is definitely of the genus *Morus*, and in size it corresponds very closely with the type fragment. It is about as large as *Sula nebouxi* with which it is here compared. Weathering of the specimen has taken away much detail.

The shaft of the bone is heavier and tapers more gradually from the expanded head toward the elbow. The caput humeri is more broadly rounded and the great pneumatic fossa is more sharply overhung on the axial side but less so on the lateral border. The fossa as a whole is smaller and the pneumatic foramen at the bottom of it is smaller and is not cribriform. The total length of the fragment is 91 mm., the diameters at the smallest point in the shaft are  $9.2 \times 7.6$  mm.

*Morus* sp.

A second solid specimen in the collection is a proximal fragment of the ulna from a gannet as large or slightly larger than *Morus bassana*, which in turn is 30 per cent larger than *M. vagabundus* as measured by Wetmore. Details have been lost, but the specimen is definitely of the genus *Morus* and is much less pneumatic than any of the boobies at hand. In *Sula nebouxi* there is a large pneumatic foramen under the palmar lip of the external cotyla and a smaller one similarly located under the internal cotyla. Both of these foramina are lacking in the fossil specimen. Post-mortem wear has obscured finer details of ligamental attachments.

## ANSERIFORMES

*Branta* sp.

A single fragment, the proximal end of an ulna, is assigned to the genus *Branta* which it resembles more closely than it does either *Anser* or *Chen*. The goose, *Presbychen abavus*, described by Wetmore from Sharktooth Hill, was a large bird, "intermediate in dimension between the largest of Canada geese and the whistling swan."

The fragment in hand is far too small to represent Wetmore's species. The specimen is too imperfect to encourage specific assignment.

## CHARADRIIFORMES

*Recurvirostra* sp.

The distal third of an ulna in the collection represents a shore bird which is not appreciably different from the Avocet (*Recurvirostra americana*). Stilt, curlew, plover, godwit, oyster-catcher, gull—all are different. In fact, if the bone were from a Recent Indian midden, it would be assigned without hesitation to *Recurvirostra americana* ♀. There are not sufficient characters to the distal end of the ulna in the great and diversified group of the shore birds to encourage me to be more specific in the assignment.

The importance of the specimen lies in the suggestion that there were shallows or sand bars in the general area at the time of deposition.

## THE MIOCENE PICTURE

During parts of the Miocene, much of Pliocene time and possibly longer, the present San Joaquin Valley was a great inland sea bordering the Sierra Nevada on the continental side and cut off from the open Pacific to the westward by the low but probably rising Coast Range. This western barrier may have been interrupted at one or more places as, for example, through the Cuyama region, but the barrier was nevertheless effective. The deposit at Sharktooth Hill suggests a minor tidal basin along the eastern border of this sea such as one finds today along the eastern shore of the Gulf of California, for example, in the region of Tapolobampo or of Mazatlán.

Whales, sea lions, sharks and maritime birds help to sketch in a picture of a fairly shallow embayment into which tidal currents eddied quietly through many years of Miocene time. Drifting in from deeper waters or floating off of nearby sand bars, the carcasses of various vertebrates accumulated here to finally settle to the bottom of relatively quiet waters. Some skeletons were completely disarticulated, others were less so. Regrettably, the birds have yielded only single elements thus far. Without optimism the paleontologist would not long survive. May we not hope then that the future will bring us more complete pictures of the birds from Sharktooth Hill?

## SUMMARY

After thirty years' neglect the Sharktooth Hill Miocene quarry has yielded a small increment of bird remains. Two specimens represent earlier described species, two new species of shearwater are described, and other fragments are assigned to two genera heretofore unrepresented from the formation, *Branta* and *Recurvirostra*. The significance of the avifauna is discussed.

*Department of Zoology, University of California, Davis, California, March 2, 1961.*

## LIPIDS IN THE LOCOMOTOR MUSCLES OF BIRDS

FRANK A. HARTMAN and KATHARINE A. BROWNELL

Fat content in locomotor muscles is an important source of energy, especially during sustained activity (George and Jyoti, 1957). The amount of such fat varies with different species, but whether this depends upon the use made of these muscles or other factors is uncertain. George and Naik (1960) reported values for the pectoralis major of birds ranging from 2.18 to 6.35 per cent in 18 species.

Hoping to throw more light on this question, we have conducted the present investigation. A comparative study of the weights of the locomotor muscles gave us the opportunity to determine the fat or lipid content of the muscles in a large number of species of birds. Our study included muscles of the lower extremities as well as the pectoralis. We have determined muscle lipids in 104 species representing 42 families.

## ACKNOWLEDGMENTS

This work was supported by a grant from the Comly-Coleman Fund of Ohio State University. We are indebted to Dr. Carl Johnson, director of the Gorgas Memorial Laboratory, Panamá, for the facilities of the Juan Mina Field Station. We also wish to thank Mr. Pablo Brackney for the use of facilities at the finca "Palo Santo" near the village of El Volcán.

## METHODS

All specimens were kept in plastic waterproof bags to prevent drying until they reached the field station. Approximately one gram samples of the muscle free from any macroscopic fat deposits were weighed accurately on a sensitive torsion balance. The muscle was cut into small pieces and dropped into redistilled ethyl alcohol and kept there until the time for analysis. Lipids (these include fats and a small quantity of other compounds soluble in the solvents used) were determined by grinding the muscle to a pulp with sand and then extracting thoroughly with a boiling 3 to 1 alcohol-ether mixture as outlined by Bloor (1943). After removal of the solvent, the residue was extracted with boiling petroleum ether. The ether was removed and the residue, determined gravimetrically, reported as total lipid.

All birds except the Japanese Quail, Indigo Bunting and Field Sparrow were collected in Panamá in December and January near sea level and in February and March at 4300 feet above sea level. The Japanese Quail were raised in the laboratory, whereas the other two species were collected in Ohio in June.

## RESULTS

Our results (see table 1) have been grouped by families since species of the same family are likely to have similar habits of activity. Taxonomic arrangement is according to Eisenmann (1955). We shall consider the pectoralis first because that is the most important muscle for locomotion.

## PECTORALIS MUSCLE

Many birds show a high lipid content of the pectoralis superficialis (p. major). These are: Least Grebe, Olivaceous Cormorant, Cattle Egret, Boat-billed Heron, parrots, Barn Owl, Lesser Nighthawk, hummingbirds, Amazon and Green kingfishers, White-ruffed Manakin, Gray-breasted Martin, Red-legged Honeycreeper, Shining Honeycreeper and Slate-throated Redstart.

The lipid content of this muscle was very low in a few species. These are: Hook-billed Kite, Barred Forest Falcon, Chestnut-winged Chachalaca, Black and White Owl

TABLE 1  
PER CENT OF LIPIDS IN LOCOMOTOR MUSCLES OF BIRDS

Tinamidae	
<i>Crypturellus soui</i> (Little Tinamou):	pectoralis, 4.27, 4.56; thigh, 1.25.
Podicipedidae	
<i>Podiceps dominicus</i> (Least Grebe):	pectoralis, 5.12.
Phalacrocoracidae	
<i>Phalacrocorax olivaceus</i> (Olivaceous Cormorant):	pectoralis, 5.30, 6.72; thigh, 4.08, 4.87.
Anhingidae	
<i>Anhinga anhinga</i> (Anhinga):	pectoralis, 3.53.
Ardeidae	
<i>Casmerodius albus</i> (Common Egret):	pectoralis, 3.78; thigh, 2.52.
<i>Leucophoyx thula</i> (Snowy Egret):	pectoralis, 4.21; thigh, 3.21.
<i>Bubulcus ibis</i> (Cattle Egret):	pectoralis, 4.99, 6.17, 7.33; thigh, 4.88.
<i>Tigrisoma lineatum</i> (Banded Tiger-heron):	pectoralis, 3.05.
<i>Ixobrychus exilis</i> (Least Bittern):	pectoralis, 2.91; thigh, 2.92.
Cochleariidae	
<i>Cochlearius cochlearius</i> (Boat-billed Heron):	pectoralis, 5.28.
Anatidae	
<i>Anas discors</i> (Blue-winged Teal):	pectoralis, 4.78.
<i>Aythya affinis</i> (Lesser Scaup):	pectoralis, 3.15, 4.45; thigh, 2.22, 3.12.
Accipitridae	
<i>Chondrohierax uncinatus</i> (Hook-billed Kite):	pectoralis, 1.04, 2.39, 2.73; thigh, 1.10.
<i>Buteo platypterus</i> (Broad-winged Hawk):	pectoralis, 3.22; thigh, 2.98.
Falconidae	
<i>Micrastur ruficollis</i> (Barred Forest Falcon):	pectoralis, 2.83; thigh, 2.21.
Cracidae	
<i>Ortalis garrula</i> (Chestnut-winged Chachalaca):	pectoralis, 1.94, 2.00, 2.04; thigh, 2.25.
Phasianidae	
<i>Odontophorus guttatus</i> (Spotted Wood Quail):	pectoralis, 1.96, 3.87.
<i>Coturnix coturnix</i> (Japanese Quail):	pectoralis, (11) 3.23±0.19 (S.E.); thigh, (10) 2.30±0.15.
Rallidae	
<i>Aramides cajanea</i> (Gray-necked Wood Rail):	pectoralis, 2.52, 2.70, 4.62; thigh, 2.23, 2.34, 3.68.
<i>Laterallus albigularis</i> (White-throated Crane):	pectoralis, 2.68, 2.76, 2.94, 3.53; thigh, 2.82, 3.16, 4.25.
Heliornithidae	
<i>Heliornis fulica</i> (Sungrebe):	pectoralis, 2.83.
Jacaniidae	
<i>Jacana spinosa</i> (American Jacana):	pectoralis, 2.99, 3.60, 4.07, 4.51, 4.95; thigh, 1.52, 2.68, 3.28.
Columbidae	
<i>Columba speciosa</i> (Scaled Pigeon):	pectoralis, 3.90, 4.14, 4.76; thigh, 2.22, 3.15, 4.08.
<i>Columba albalinea</i> (White-naped Pigeon):	pectoralis, 4.47, 5.10, 5.11; supracoracoideus, 2.40; thigh, 2.72, 3.60, 5.34.
<i>Columba subvinacea</i> (Ruddy Pigeon):	pectoralis, 3.30; thigh, 3.00.
<i>Columbigallina talpacoti</i> (Ruddy Ground Dove):	pectoralis, 2.99, 3.08, 3.31, 3.56.
<i>Claravis pretiosa</i> (Blue Ground Dove):	pectoralis, 2.23, 3.50, 3.64, 4.23.
<i>Leptotila verreauxi</i> (White-tipped Dove):	pectoralis, 2.62.
<i>Leptotila cassinii</i> (Gray-chested Dove):	pectoralis, 1.81, 2.80; thigh, 5.81, 6.45.
<i>Leptotila rufinucha</i> (Rufous-naped Dove):	pectoralis, 2.33; thigh, 1.73.
<i>Geotrygon chiriquensis</i> (Rufous-breasted Quail Dove):	pectoralis, 2.48, 2.50.
Psittacidae	
<i>Brotogeris jugularis</i> (Orange-chinned Parakeet):	pectoralis, 4.81, 5.03, 5.27.
<i>Pionopsitta haematotis</i> (Brown-hooded Parrot):	pectoralis, 5.00, 5.57, 5.72; thigh, 3.35, 3.73, 4.10.
<i>Amazona autumnalis</i> (Red-lored Parrot):	pectoralis, 4.90.

## Cuculidae

*Crotophaga ani* (Smooth-billed Ani): pectoralis, 3.27, 3.85.

## Tytonidae

*Tyto alba* (Barn Owl): pectoralis, 5.40; thigh, 1.93.

## Strigidae

*Otus choliba* (Tropical Screech Owl): pectoralis, 2.76.

*Ciccaba nigrolineata* (Black and White Owl): pectoralis, 2.10; thigh, 1.80.

*Rhinoptynx clamator* (Striped Owl): pectoralis, 3.10.

## Nyctibiidae

*Nyctibius griseus* (Common Potoo): pectoralis, 2.56, 3.86.

## Caprimulgidae

*Chordeiles acutipennis* (Lesser Nighthawk): pectoralis, 6.94.

*Nyctidromus albigollis* (Parauque): pectoralis, 3.78, 3.86.

## Trochilidae

*Camptyllopterus hemileucurus* (Violet Sabrewing): pectoralis, 4.50, 4.66, 5.06, 5.18, 5.23, 5.32; heart 4.20, 5.66.

*Phaeochroa cuvierii* (Scaly-breasted Hummingbird): pectoralis and supracoracoideus, 5.24, 5.31.

*Damophila julie* (Violet-bellied Hummingbird): pectoralis and supracoracoideus, 5.05, 5.39, 5.62.

*Amazilia tzacatl* (Rufous-tailed Hummingbird): pectoralis and supracoracoideus, 4.72.

*Lampornis castaneiventris* (White-throated Mountain Gem): pectoralis and supracoracoideus, 5.05.

## Trogonidae

*Pharomachrus mocinno* (Quetzal): pectoralis, 3.55, 3.93.

*Trogon strigilatus* (White-tailed Trogon): pectoralis, 2.99, 3.40; thigh, 5.32, 7.12.

*Trogon rufus* (Black-throated Trogon): pectoralis, 3.77.

*Trogon violaceus* (Violaceous Trogon): pectoralis, 3.56.

## Alcedinidae

*Ceryle torquata* (Ringed Kingfisher): pectoralis, 3.72; thigh 4.08.

*Chloroceryle amazona* (Amazon Kingfisher): pectoralis, 4.49, 4.76, 5.32.

*Chloroceryle americana* (Green Kingfisher): pectoralis, 4.15, 4.42, 5.27.

## Momotidae

*Momotus momota conexus* (Blue-crowned Motmot): pectoralis, 2.04.

*Momotus momota lessonii*: pectoralis, 3.91.

## Capitonidae

*Eubucco bourcierii* (Red-headed Barbet): pectoralis, 3.23.

*Semnorhis frantzii* (Prong-billed Barbet): pectoralis, 2.91; thigh, 3.40, 3.80.

## Ramphastidae

*Pteroglossus torquatus* (Collared Araçari): pectoralis, 2.92.

*Pteroglossus frantzii* (Fiery-billed Araçari): pectoralis, 3.15; thigh, 3.25.

*Ramphastos swainsonii* (Chestnut-mandibled Toucan): pectoralis, 2.78; thigh, 1.93.

## Picidae

*Picumnus olivaceus* (Olivaceous Piculet): pectoralis, 3.84, 3.86.

*Piculus rubiginosus* (Golden-olive Woodpecker): pectoralis, 4.14; thigh, 3.11.

*Dryocopus lineatus* (Lineated Woodpecker): pectoralis, 3.54, 3.63; thigh, 3.15.

*Centurus rubricapillus* (Red-crowned Woodpecker): pectoralis, 3.09, 4.07; thigh, 5.85, 6.32.

*Centurus pucherani* (Black-cheeked Woodpecker): pectoralis, 3.42, 4.10; thigh, 4.39, 4.73.

*Phloeocastes melanoleucos* (Crimson-crested Woodpecker): pectoralis, 3.22, 3.60; thigh, 2.20, 3.39.

## Dendrocolaptidae

*Xiphorhynchus guttatus* (Buff-throated Woodhewer): pectoralis, 2.46; thigh, 5.09.

*Lepidocolaptes affinis* (Spot-crowned Woodhewer): pectoralis, 2.78, 2.80.

## Furnariidae

*Synallaxis brachyura* (Slaty Spinetail): pectoralis, 3.40.

*Anabacerthia striaticollis* (Scaly-throated Foliage-gleaner): pectoralis, 4.20.

## Formicariidae

- Cymbilaimus lineatus* (Fasciated Antshrike): pectoralis, 2.56.  
*Thamnophilus dolatus* (Barred Antshrike): pectoralis, 2.81.  
*Dysithamnus mentalis* (Plain Antvireo): pectoralis, 3.40.  
*Cercomacra tyrannina* (Dusky Antbird): pectoralis, 3.99.

## Pipridae

- Corapipo leucorrhoa* (White-ruffed Manakin): pectoralis, 5.11.  
*Manacus vitellinus* (Golden-crowned Manakin): pectoralis, 4.32.

## Cotingidae

- Tityra semifasciata* (Masked Tityra): pectoralis, 4.45.  
*Querula purpurata* (Purple-throated Fruitcrow): pectoralis, 3.69.

## Tyrannidae

- Miodynastes maculatus* (Streaked Flycatcher): pectoralis, 2.89, 3.01; thigh, 3.45.  
*Megarhynchus pitangua* (Boat-billed Flycatcher): pectoralis, 3.42; thigh, 2.80.  
*Rhynchocyclus brevirostris* (Eye-ringed Flatbill): pectoralis, 2.72, 2.75.  
*Lophotriccus pileatus* (Scale-crested Pygmy Tyrant): pectoralis, 3.75.  
*Elaenia frantzii* (Mountain Elaenia): pectoralis, 4.04.  
*Myiobagis viridicata* (Greenish Elaenia): pectoralis, 3.71.

## Hirundinidae

- Progne chalybea* (Gray-breasted Martin): pectoralis, 5.50, 6.00, 6.31.

## Troglodytidae

- Thryothorus modestus* (Plain Wren): pectoralis, 3.27.

## Turdidae

- Turdus plebejus* (Mountain Robin): pectoralis, 3.18; thigh, 2.24.  
*Hylocichla ustulata* (Olive-backed Thrush): pectoralis, 3.81.

## Coerebidae

- Cyanerpes cyaneus* (Red-legged Honeycreeper): pectoralis, 4.56.  
*Cyanerpes lucidus* (Shining Honeycreeper): pectoralis, 4.90, 5.46, 5.70, 6.24.

## Parulidae

- Myioborus miniatus* (Slate-throated Redstart): pectoralis, 4.89.

## Icteridae

- Zarkhynchus wagleri* (Chestnut-headed Oropendola): pectoralis, 3.18, 3.89; thigh, 2.24, 3.44.

## Thraupidae

- Tangara larvata* (Golden-masked Tanager): pectoralis, 3.60, 3.81.  
*Tangara gyrola* (Bay-headed Tanager): pectoralis, 3.55.  
*Thraupis virens* (Blue-gray Tanager): pectoralis, 3.64.  
*Piranga rubra* (Summer Tanager): pectoralis, 3.70.  
*Chlorospingus ophthalmicus* (Common Bush Tanager): pectoralis, 3.00, 3.88.

## Fringillidae

- Saltator albicollis* (Streaked Saltator): pectoralis, 3.20.  
*Pheucticus ludovicianus* (Rose-breasted Grosbeak): pectoralis, 3.99, 4.28.  
*Passerina cyanea* (Indigo Bunting): pectoralis, 3.85; thigh, 3.83; heart, 1.31.  
*Arremonops conirostris* (Green-backed Sparrow): pectoralis, 2.25.  
*Spizella pusilla* (Field Sparrow): pectoralis, 2.44.

and Blue-crowned Motmot. The lipid values of the others lay between these high and low groups.

Usually lipid content in individuals of the same species agreed fairly well. Occasionally one specimen would be very low. In the family Ardeidae, there is considerable range in lipid values of the pectoralis (2.91 to 7.33 per cent), that for the Cattle Egret being extremely high. Likewise in the Columbidae the range is great (1.81 to 5.11 per cent). In the Caprimulgidae, the lipid content in the Lesser Nighthawk was much higher than that in the Parauque. All species of the Trochilidae possessed high lipid contents in the

combined pectoralis and supracoracoideus muscles (combination necessary to obtain enough tissue for analysis). The lipid content of the pectoralis was higher in *Momotus momota lessonii* than in *Momotus momota conexus*. The values in the different Picidae were not far apart, while in the Tyrannidae the range was somewhat greater. Pectoralis lipids checked closely for the different species of Thraupidae but not so closely for members of the Fringillidae.

In connection with pectoral lipid determination in the hummingbird, we made lipid determinations of the heart in two specimens of *Campylopterus hemileucurus*. We found it to be almost as high in the heart as in the pectoralis, or even higher. The values in each individual were: bird A—heart lipid, 4.20 per cent, pectoral lipid, 4.50 per cent; bird B—heart lipid, 5.66 per cent, pectoral lipid, 4.66 per cent.

#### THIGH MUSCLE

Lipids of the thigh were determined in a much smaller number of species than those in which values for lipids were obtained for the pectoralis. The values were often different from those for the pectoralis. They were high in the Olivaceous Cormorant, Cattle Egret, White-naped Pigeon, Gray-chested Dove, White-tailed Trogon, Ringed Kingfisher, Red-crowned Woodpecker, Black-cheeked Woodpecker, and Buff-throated Woodhewer. They were low in the Little Tinamou, the Hook-billed Kite, the Rufous-naped Dove, the Barn Owl and the Black and White Owl. Although only scattered determinations were made, thigh lipids were most often equal to or less than pectoral lipids. They were less in the Little Tinamou, the Olivaceous Cormorant, the Common Egret, the Snowy Egret, Cattle Egret, the Lesser Scaup, the Hook-billed Kite, the Barred Forest Falcon, the Japanese Quail, the American Jacana, the Rufous-naped Dove, the Brown-hooded Parrot, the Barn Owl, the Chestnut-mandibled Toucan, the Golden-olive Woodpecker, the Lineated Woodpecker, the Boat-billed Flycatcher and the Mountain Robin. They were greater in the Gray-chested Dove, the White-tailed Trogon, the Prong-billed Barbet, the Red-crowned Woodpecker, the Black-cheeked Woodpecker, the Buff-throated Woodhewer, the Streaked Flycatcher and the Yellow-billed Cacique. Some of these comparisons were made between different individuals, but in many instances the comparative data came from the same individual.

#### DISCUSSION

In this preliminary survey of representative members of several families, it is evident that the amount of lipid in the muscles of locomotion varies considerably. It may be similar in members of the same family or occasionally quite divergent. Within the species the values tend to be close for the various individuals but here again there are exceptions. Usually the amount of lipid is high in muscles accustomed to sustained activity. But it may also be high in species not noted for prolonged exercise as for example the pectoralis in the Little Tinamou and the Barn Owl. Why the lipid concentration in the thigh of the White-tailed Trogon and the Ringed Kingfisher is high is difficult to understand on the basis of use.

What are the possible factors involved in lipid concentration in these muscles? Fats absorbed from the alimentary canal or produced from other food stuffs are stored in depots of various parts of the body, some being found in the liver where it is processed, and some in the muscles themselves.

The fat in the muscle can be utilized there, since George and Scaria (1956) found high lipase activity in the pectoralis. Evidence for its use was demonstrated by George and Jyoti (1955) by stimulating the pectoralis and leg muscles electrically until fatigued, or by forcing pigeons to fly in a large hall, or by starving pigeons for one week. They

observed that the muscle fibers lost their fat globules but that their utilization during starvation was secondary. In other words, muscle fiber fat was used primarily for muscle work. Later George and Jyoti (1957) reported that when the pectoral muscle was electrically stimulated, of the total energy expended, 71 per cent in the pigeon and 61 per cent in the kite and fowl were derived from fat. The breast muscle in the kite was fatigued more quickly.

George and Naik (1960) published lipid values for the pectoralis in two birds which differed markedly from ours. For the Cattle Egret they obtained a mean of 3.90 per cent for 4 specimens (maximum, 4.14 per cent) whereas our values for the same species were 6.20 per cent for 3 specimens (maximum, 7.33 per cent). In the Barn Owl they obtained 3.69 per cent for one specimen whereas our value was 5.40 per cent for a single specimen. It is difficult to account for these discrepancies. Their method differed from ours in that our final extraction contained only the substances soluble in boiling petroleum ether. Our values should have been lower than theirs since some substances were eliminated by the last extraction. Difference in diet might be a factor. However, there is no evidence for this.

In a preliminary experiment we took eight mature Japanese Quail hatched at the same time, 48 days before. All birds were fed "Game Bird Growena" for 30 days, four of them receiving the same type of feed to which 10 per cent fat had been added. At the end of the period, lipid determinations were made on the pectoralis and thigh muscles. There was no significant difference between the values in the fat fed and the control birds. Perhaps a larger group of birds would show a difference.

It is noteworthy that the lipid content of the heart in the hummingbird is similar to that of pectoralis plus supracoracoideus. The heart in this species must meet increased demands several hours a day. The pectoralis is required to do the same. The heart also must beat throughout the life of the individual.

The importance of the presence of lipid or fat in skeletal muscle has not been fully appreciated. It represents a reserve which is more readily available for immediate use than that in the more remote fat depots. It is a constant constituent of locomotor muscles. Birds that use their wings in power flight for long periods possess high or fairly high lipid content in the pectoralis muscles. Although some species that are not very active also show high pectoral lipid content, the important fact is that the very active birds usually have a high lipid reserve.

#### SUMMARY

The lipid content of the pectoralis was determined in 104 species of birds representing 42 families. All but three species were collected in Panamá.

Most species showed a high lipid content of the pectoralis, only a few showed a low content. Different individuals of the same species usually agreed fairly well. Differences between species in the same family were sometimes of a considerable range. This was true for Ardeidae, Columbidae, Caprimulgidae, and Momotidae. Pectoralis lipid corresponded closely in the different species of Picidae and Thraupidae. The lipid content of the heart in a hummingbird was almost as high or higher than that in the pectoralis and supracoracoideus combined.

The lipids of the thigh muscles were sometimes different from those in the pectoralis. They were high in some and low in others. More often they were equal to or less than pectoral lipids.

Usually the lipid concentration is high in muscles acting to sustain activity, but it may also be high in species not noted for prolonged activity.



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LATE SPRING OBSERVATIONS ON BIRDS OF SOUTH FARALLON ISLAND,  
CALIFORNIA

By ROBERT I. BOWMAN

The Farallon Islands, situated about 27 miles west of San Francisco, have long attracted the attention of ornithologists because of their enormous breeding colonies of sea birds and the rather frequent occurrence there of land birds otherwise rare to California (see Cooper, 1868; Townsend, 1885; Bryant, 1888; and Dawson, 1911*b*). Because of the fact that for over 25 years there has been no published report on the late spring bird life of the Farallones, the writer arranged for a visit to South Island from June 10 to 17, 1958.

I wish to thank the following persons from San Francisco State College for permission to use here certain of their field observations: Helen Deman, Richard Grill, Kenneth Hinde, Carl Johnson, Morton Keston, and Norman McLean. Transportation and living accommodations for our group were provided through the courtesy of the 12th Coast Guard District.

The following unusual species were collected (specimens deposited in the Vertebrate Museum, San Francisco State College):

*Oporornis agilis*. Connecticut Warbler. An adult male showing a rather heavy deposit of subcutaneous fat and a moderately enlarged testis,  $4.5 \times 2.5$  mm., was taken on June 16. I am unaware of any previous record of this species for California.

*Seiurus aurocapillus aurocapillus*. Ovenbird. An adult male with an enlarged testis,  $7.0 \times 4.5$  mm., was collected on June 17. There is one previous record of this species from the Farallon Islands (Dawson, 1911*a*) in addition to four other records from southern California (see Grinnell and Miller, 1944:408-409; and Jaeger, 1947:244).

*Dendroica pensylvanica*. Chestnut-sided Warbler. An adult female, as determined by plumage, was taken on June 17. Previous records of this species for California include an immature male from Mendocino County, September 21 (Marsden, 1909:64); an immature of unknown sex from Marin County, September 24 (Kinsey, 1947); and a female of unknown age from Imperial County, October 5 (Cardiff and Cardiff, 1953:217).

*Vireo olivaceus*. Red-eyed Vireo. An adult female, containing several ova measuring 1.0 mm. in diameter, was taken on June 16. There are but two previous records of this species for California, both in October (see Grinnell and Miller, 1944:388).

The following passeriform birds are reported on the basis of field observations only: 1 Lesser Goldfinch (*Spinus psaltria*), June 11; 5 House Finches (*Carpodacus mexicanus*), June 11; 1 Brown-headed Cowbird (*Molothrus ater*), June 16; 1 female House Sparrow (*Passer domesticus*) feeding young, June 15; 1 female American Redstart (*Setophaga ruticilla*), June 16; 1 male Yellowthroat (*Geothlypis trichas*), June 13; 1 Swainson Thrush (*Hylocichla ustulata*), June 17; numerous Rock Wrens (*Salpinctes obsoletus*), including two discovered roosting together in a shallow concavity at the end of a wooden beam supporting a water tank, on June 13; 1 Red-breasted Nuthatch (*Sitta canadensis*), June 15; 1 Olive-sided Flycatcher (*Nuttallornis borealis*), June 16; and 1 Western Flycatcher (*Empidonax difficilis*), June 17.

Except for the Rock Wren, House Sparrow, and House Finch, which are known to breed on the island, all species just mentioned may be considered to be vagrants or transients. So far as we could determine, each species was represented by but one individual, and most of them made their appearance during the last three days of our visit (June 15 to 17) when there was almost continuous fog about the island and the adjacent mainland, with very little wind. The birds were obviously confused as they first appeared in the vicinity of two Monterey cypresses which were the only trees



Fig. 1. Views of South Farallon Island, June, 1958.

A. Coast Guard installations, southeast end. Stone wall around rain apron is the favorite nesting site of petrels. Vagrant land birds were noted chiefly in the two Monterey cypress trees beside the house. Seal rocks are in the background.

B. Main colony of Brandt Cormorants on north terrace between Shubrick Point and Tower Point. Sugar-loaf Island is at the far right.

C. Nesting grounds of the Western Gull are to the west of the old Keeper's House. Light house peak is in the background.

D. Small portion of a breeding colony of Common Murres at West End. To the right is Indian Head.

on the island (fig. 1a). For example, the Ovenbird was first seen on the ground beneath the cypress trees, from which point it flew eastward about 200 yards; then suddenly it made a complete turnabout returning to within 100 yards of the trees, finally landing on a rocky slope barren of vegetation. About 15 minutes later the same individual flew back to the trees and was collected for us by Coast Guard personnel. Likewise the Yellowthroat flew back and forth between the ground and the trees during the very brief period that it was observed before disappearing in the fog. It was a most peculiar sight to see such species as the House Finch, House Sparrow, Redstart, Yellowthroat, Chestnut-sided Warbler, Ovenbird, Swainson Thrush, and Western Flycatcher, many

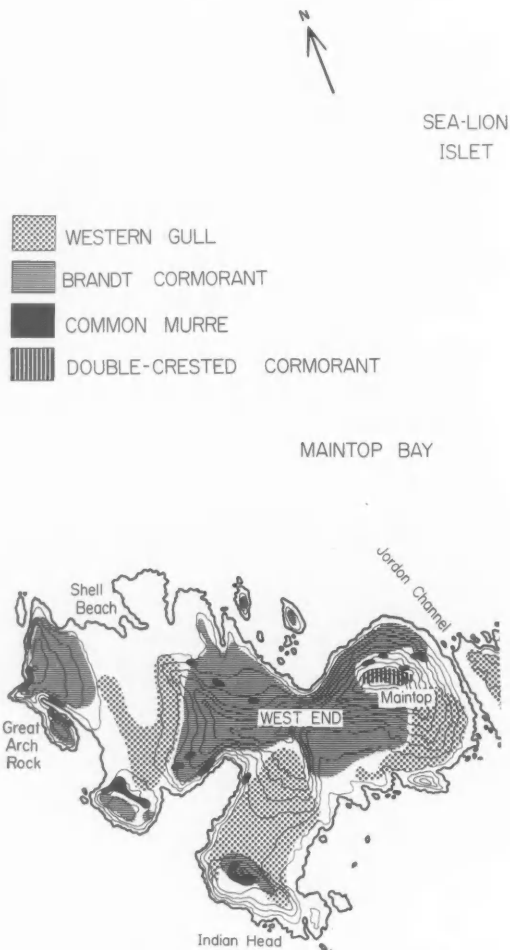


Fig. 2. Map of South Farallon Island and adjacent rocks showing the distribution of the principal breeding colonies of four species of sea birds, June 10 to 17, 1958. Scale, 1 inch to approximately 175 yards. Sea-lion Islet is first to the right of the printed name.

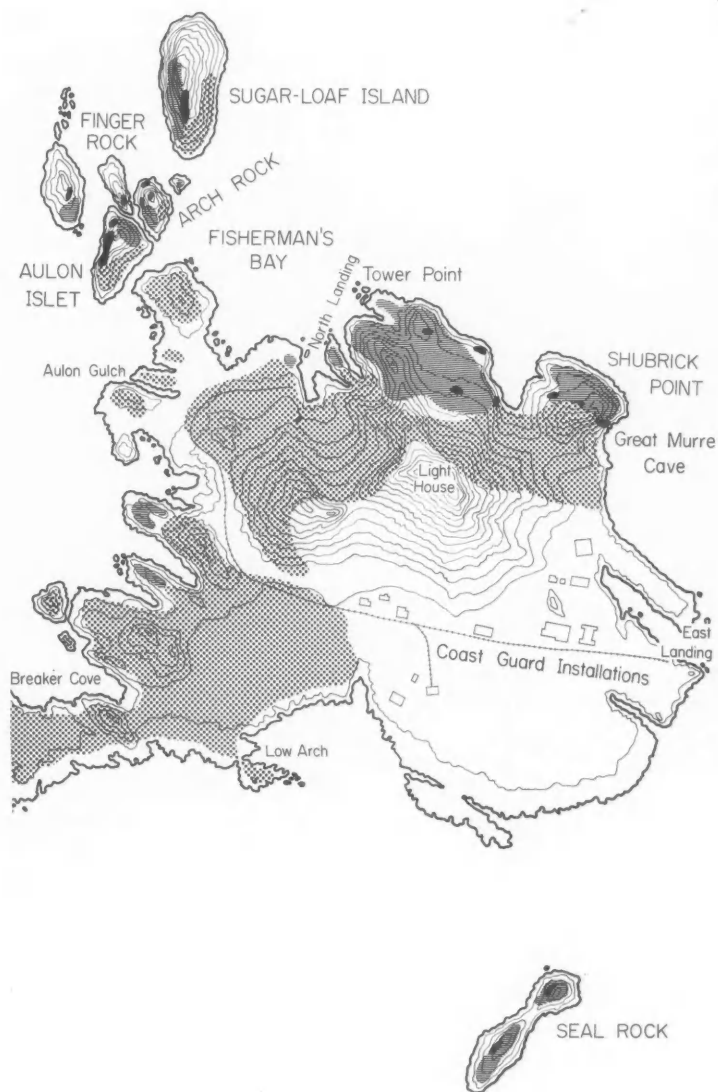


Fig. 2 continued. See opposite page.

with rather dissimilar ecologic requirements, moving about in the same tree at the same time on the morning of June 17.

The feathered remains of a Burrowing Owl (*Speotyto cunicularia*) and a Glaucous Gull (*Larus hyperboreus*) were found on the south side of the island some distance from shore. There is only one previous record of the Glaucous Gull from the Farallon Islands (Cooper, 1868:9).

As a basis for future studies, a few estimates of the size of the sea-bird populations were made and the locations of the principal breeding colonies were plotted on a large-scale map of the island (fig. 2).

*Oceanodroma leucorhoa beali*. Leach Petrel. Previous reports of this petrel on the Farallones were made by Loomis (1896:359) and Dawson (1911b:176), both of whom found breeding adults in late spring and early summer. On June 15, 1958, we captured three individuals as they were about to enter crevices in the rock walls which enclose the large rain apron on the south side of the island (fig. 1a). A single bird was banded and released and two were saved as study skins.

*Oceanodroma homochroa*. Ashy Petrel. Thousands of petrels were seen or heard about the island after dark. On clear evenings the first birds would make their appearance from over the ocean about 40 minutes after sunset. The number of birds in flight seemed to reach a peak around midnight on June 14. Many petrels were captured by hand as they landed on the ground. Nests were situated in the stone walls, in rock piles, under boards, and beneath barracks. There were few areas visited after dark where petrels were not detected. Their presence was indicated by faint gurgling sounds or by strong musky odors. Sixteen Ashy Petrels were banded on June 14 and 15. A bird captured on June 15 was prepared as a study skin. Fresh eggs were noted in three nests on June 14, and a very young nestling was discovered on June 17.

*Pelecanus occidentalis*. Brown Pelican. From an observation point on Arch Rock about 75 pelicans were visible atop Sugar-loaf Island (fig. 2). Because of the angle of observation and the distance involved, it was not possible to determine with absolute certainty if the birds were nesting; but a few shallow mounds scattered about the slopes between the sitting birds were suggestive of nests. If, in fact, Brown Pelicans do breed on the Farallones, it would constitute the northernmost breeding station in California (see Grinnell and Miller, 1944:51). There is one previous report of this species on the Farallones (Bryant, 1888:41). A left humerus, matching that of a Brown Pelican, was found by our group on South Island.

*Phalacrocorax auritus*. Double-crested Cormorant. This cormorant, the largest of the three species breeding on the island, was found only on the ridge of Maintop at West End where over 50 attended nests were counted. It is unknown if eggs or young were present since a closer approach, it was feared, might have frightened the birds from their nests, exposing their contents to the predatory Western Gulls. In 1911, between May 20 and June 3, Dawson (1911b:177) counted about 35 pairs (15 nests) on Maintop.

*Phalacrocorax penicillatus*. Brandt Cormorant. This was the commonest and most widely distributed cormorant on South Farallon Island. The greatest concentration of breeding birds was situated on the gently sloping sea terrace between Tower Point and the lighthouse where approximately 1000 nests were counted (fig. 1b). Eggs were present in most of these nests. Nesting colonies were generally situated on north-facing slopes and thus were exposed to the full sweep of the prevailing northwest winds. Such locations are probably preferred by these large black birds because they are cooler and permit easier takeoffs and landings. The first young, only a day or two old, was noted on June 15. Nests were composed of dried Farallon weed (*Baeria maritima*) and algae.

Most of the guano deposits on West End are probably due to the Brandt Cormorant. Even though this avian fertilizer was once harvested commercially (Barlow, 1897), extensive deposits still remain. Some deposits are as much as 10 inches deep.

*Phalacrocorax pelagicus*. Pelagic Cormorant. In marked contrast to the two previous species which are colonial nesters, the Pelagic Cormorant is largely a solitary nester. Breeding birds were found mainly on inaccessible ledges at the northeast end of the island and at the east side of Maintop (West End). No young were seen.

*Haemantopus bachmani*. Black Oystercatcher. Although reported to have disappeared from the

Farallon Islands where it was once known (Grinnell and Miller, 1944:134), our group estimated that there were about 12 pairs resident on South Island in mid-June, 1958. The species was heard and seen regularly. One nest, composed of small pebbles and containing three fresh eggs, was found near East Landing on June 17.

*Larus occidentalis*. Western Gull. No other species was so conspicuous and ubiquitous as the Western Gull (fig. 1c). Nests were absent only from those areas occupied by cormorant or murre colonies or those immediately adjacent to Coast Guard installations (fig. 2). Most of the young were no more than ten days old.

*Uria aalge*. Common Murre. Early reports of this species (Bryant, 1888) state that the murre is by far the commonest nesting sea bird on the Farallones, outnumbering all other species combined! Indeed, the birds were so plentiful during the latter part of the 19th century that they supported a large commercial egg industry that operated out of San Francisco (Loomis, 1896). Smith (1934:171) who was the last observer to report on the nesting population of murre, noted no more than 30 adults on South Island in August, 1933. In mid-June, 1958, small groups of 5 to 20 birds were found nesting in caves and on ledges at several points (see fig. 2). The bulk of the population was centered along the westernmost cliffs of West End where we estimated that over 2000 birds were attending eggs (fig. 1d). Emerson (1904) also found murre most plentiful in this same area in 1903. On June 14 we found one young estimated to be less than two days old. The large colony that formerly inhabited Great Murre Cave near Shubrick Point, was not intact in 1958. Only 30 birds were observed there on June 10. Small colonies occurred on the two peaks of Seal Rock (fig. 2).

*Cephus columba*. Pigeon Guillemot. Individuals were observed in rocky crevices, in burrows of the European rabbit (*Oryctolagus*), and beneath railroad ties. The principal nesting sites were in the vicinity of Shubrick Point and the large surge channel immediately south of East Landing. Although most of the birds were found sitting on eggs in burrows, on June 15 a bird was observed incubating a single egg upon an exposed ledge. The largest group contained 10 birds.

*Ptychoramphus aleutica*. Cassin Auklet. Locally called "night-birds," the Cassin Auklet was observed above ground only after dark. During daylight hours numerous birds were removed from shallow burrows in the soil at the southeast end of the island. Many could be seen in rock crevices near Shubrick Point. Most of the auklets examined were sitting on single eggs. A recently hatched young was removed from a rockpile on June 15. Thirty-three adults were banded.

*Lunda cirrhata*. Tufted Puffin. Nesting puffins were probably more numerous than our observations would suggest. During the morning of June 13 approximately 20 birds were observed along the north side of Shubrick Point. Several of the birds were seen to enter crevices in the rocks wherein a single egg was found in each of five nest tunnels examined with a flashlight. One such egg removed from under an incubating puffin was found to contain a feathered embryo nearly at the hatching stage.

On May 18, 1954, the writer made a brief visit to South Island in company with Mr. George Treichel. Among the land birds observed, three species have not previously been reported from the Farallon Islands, namely, Pine Siskin (*Spinus pinus*), Horned Lark (*Eremophila alpestris*), and Black Phoebe (*Sayornis nigricans*).

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*Department of Biology, San Francisco State College, San Francisco, California,  
November 25, 1960.*



## FROM FIELD AND STUDY

**Recent Records of Birds in Korea.**—According to Austin (Bull. Mus. Comp. Zool., 101, 1948:43), the Black-crowned Night Heron (*Nycticorax nycticorax*) is a rare straggler in Korea and known only from three records taken between 1925 and 1928; no specimens apparently, were saved. On December 17, 1960, I purchased a dead juvenal female of this species in the South Gate Market, Seoul, and preserved it as a skin. It weighed 515 gm. This is the only record of this species I have made during the past seven years of residence in Korea.

On September 15, 1956, Lt. Harvey L. Patten collected a single male Swinhoe Snipe (*Capella megala*). It was shot when flushed from a wet rice paddy along the coast of the Yellow Sea approximately 5 miles northeast of Inchon, Kyonggi-do. It weighed 160 gm. and was fat. This specimen was preserved as a skin. Identification was made by Kenneth C. Parkes of the Carnegie Museum. Austin (*op. cit.*:124) refers to this species as a rare transient in Korea and lists a total of only seven specimens taken between 1880 and 1934. To date, this is my only encounter with the species in Korea.

On January 21, 1961, I purchased two dead Ring Doves (*Streptopelia decaocto s'olichkae*) in the South Gate Market, Seoul, and saved them as skins. One was a male which weighed 174 gm. The sex of the other was not determined; it weighed 159 gm. The stomachs of both contained rice and beans. Austin (*op. cit.*:141) refers to this species as "evidently an uncommon resident of local distribution, formerly more abundant than it is today." He lists a total of 23 specimens taken between 1883 and 1929. This is the first time I have encountered the species in the past seven years of residence in Korea.

On May 31, 1960, I collected, in Seoul, a single male Arctic Willow Warbler (*Phylloscopus borealis*) of the race *examinandus*. Identification and racial determination were made by Herbert G. Deignan of the United States National Museum. The specimen was captured in a mist net on the United States Army Compound in a grassy, brushy area, sparsely wooded with chestnuts. It weighed 10 gm. The gonads were slightly enlarged and measured  $4.0 \times 4.5$  and  $3.5 \times 4.0$  mm, respectively. Austin (*op. cit.*:215) was unable to confirm the record in the 1942 Japanese Hand-List of this form for Korea and found no trace of a specimen having been taken. Accordingly, the 1958 edition of the Hand-List (p.63) states "Recorded from Korea (doubtfully once) Austin, Jr., Bds. Korea, 1948 (no specimen)." Consequently, my specimen appears to constitute the first definite record of this race for Korea.

I am grateful to Herbert G. Deignan of the United States National Museum and Richard C. Banks of the Museum of Vertebrate Zoology for assistance in the identification of specimens taken and to Harvey L. Patten for the donation of the specimen of the Swinhoe Snipe. All specimens taken are deposited in the Museum of Vertebrate Zoology.—CHESTER M. FENNELL, Seoul, Korea, January 26, 1961.

**Scaled Petrel in Oregon.**—On July 25, 1959, Leon A. Fredrich and I discovered a dead Scaled Petrel (*Pterodroma inexpectata*) on the winter high tide line of a beach two miles north of Alsea Bay, Lincoln County, Oregon. Dr. Frank Richardson of the Washington State Museum and Mr. Richard C. Banks of the Museum of Vertebrate Zoology have verified the identification of this specimen. Mr. Banks informs me that the bird agrees well with other examples "in measurements and in configuration of the bill, differing only in having more dark colored feathers on the forehead."

In regard to the distribution of the Scaled Petrel along the shores of the United States, Mr. Herbert G. Deignan of the United States National Museum states that "the Scaled Petrel was first reported from North America by William Brewster" (Bull. Nutt. Ornith. Club, 6, 1881:91-97). The specimen was collected early in 1880 at Mount Morris, Livingston County. This bird is in the Museum of Comparative Zoology.

Gabrielson and Lincoln in the "Birds of Alaska" (1959:83) report four specimens from Alaska: one taken at Kodiak on June 11, 1882; one near Sitka on May 17, 1908; one in Kiska Harbor on June 17, 1911; and a fourth found dead near the base of Frosty Peak on August 6, 1911.

The nearly complete skeleton of the specimen obtained in Oregon is now in the Museum of Vertebrate Zoology.—WILLIAM M. WALLACE, Fort Lewis, Washington, January 18, 1961.

**First Record of European Skylark on San Juan Island, Washington.**—On August 15, 1960, while crossing a field about three miles southwest of Friday Harbor, San Juan Island, Washington, my attention was suddenly directed to a brown bird which rose from the grass with an unfamiliar call note and began climbing away from me in a long arc. The generic characteristics of this bird were readily apparent through  $8\times$  binoculars as I had often seen larks of the genus *Alda* 17 years previously in North Africa. The white outer tail feathers, low crest, and relatively short tail peculiar to the European Skylark (*Alda arvensis*) were closely observed.

The lark's flight pattern was characterized by a gradual ascent to a height of 25 or 30 yards followed by a rather steep descent into the grass at a distance of 75 to 100 yards from the starting point. The bird permitted me to approach to within six or seven yards before flushing, and it circulated entirely within a 50-acre tract. The surrounding terrain encompassed several hundred acres of rolling sheep pasture divided by alder hedges and barbed wire fences. It supported a fairly dense growth of dry grass averaging about one foot in height. The predominant birds present were Western Meadowlarks (*Sturnella neglecta*) and Savannah Sparrows (*Passerculus sandwichensis*).

Apparently the seven mile width of Harro Strait has been an effective barrier in confining the European Skylark to Vancouver Island since its successful introduction there. The total distance between Friday Harbor and Saanich Peninsula, Vancouver, is about 16 miles. It is noteworthy that in Europe the Skylark is a wide-ranging species of migratory habit. A careful search of large fields on San Juan Island may reveal a few nesting pairs of this lark.—JAMES A. BRUCE, *Wooster, Ohio, December 3, 1960.*

**Recent Waterfowl Records for Colorado.**—*Oidemia nigra*. Common Scoter. One immature bird was found by Laren A. Roper and Philip L. Lee on November 24, 1960, on Watson Lake, five miles northeast of Fort Collins, Larimer County. The bird had washed ashore, apparently after being shot. The wings are in the Colorado Cooperative Wildlife Research Unit Collections. Niedrach and Rockwell (*The Birds of Denver and Mountain Parks*, 1939) considered this species an extremely rare visitant and mentioned only two records for the Denver area. Cooke (*The Birds of Colorado*, 1897) mentioned two other records for the state, one from near Fort Collins.

*Clangula hyemalis*. Oldsquaw. An immature male was found dead near Masonville in Larimer County, November 25, 1958, by T. O. Thatcher. The specimen is now in the collections of the Zoology Department, Colorado State University. Bergtold (*A Guide to the Birds of Colorado*, 1928) listed the Oldsquaw as a "rare winter straggler" in Colorado. Slater (*A History of the Birds of Colorado*, 1912) mentioned records for Denver, Fort Collins, Loveland and Longmont. Niedrach and Rockwell (*loc. cit.*) cited a few more records for the Denver area. A biologist of the Colorado Game and Fish Department noted a bird during hunters' bag checks in the Arkansas Valley of southeastern Colorado, November 7, 1950. Records of the Colorado Bird Club include sight observations of individuals seen near Fountain, November 3, 1955, and near Colorado Springs, December 29, 1956. John and Margaret Douglass observed a female Oldsquaw in winter plumage at Estes Park, December 10, 1960.

*Branta nigricans*. Black Brant. Hansen and Nelson (*Trans. N. Am. Wildl. Conf.*, 1957) reported a banded Black Brant recovered near Loveland, Colorado. Hansen (*pers. comm.*) was confident the bird recovered was correctly identified as a Black Brant at the time of banding. Mr. Johnny Price shot the goose (band no. 48-737790) at Union Reservoir near Longmont in Weld County sometime between November 1 to December 30, 1954. It had been banded in western Alaska on Nelson Island (about  $60^{\circ} 45' N$ ;  $165^{\circ} W$ ) on July 28, 1951. This apparently is the first record of the species for Colorado. Slater (*op. cit.*) lists one questionable record for *Branta bernicula*, a specimen shot at Fort Lyon, April 11, 1883, which was not preserved.—RONALD A. RYDER and LAREN A. ROPER, *Colorado State University, Fort Collins, Colorado, April 24, 1961.*

**Cassin Finch and Pine Grosbeak in West-central Kansas.**—On December 27, 1960, I collected a pair of Cassin Finches (*Carpodacus cassinii*) from a flock of eight on the Fort Hays Kansas State College campus. This species has not previously been recorded from the state. Flocks of three to 19 birds were observed at intervals throughout the winter usually in brushy vegetation bordering Big Creek or in ornamental plantings on campus. A few Purple Finches (*Carpodacus purpureus*) were occasionally present with the Cassin Finches, but in general the two species mingled very little. A singing male Cassin Finch was collected March 12, 1961, and the species is still present at this writing.

Johnston (Univ. Kans. Mus. Nat. Hist. Misc. Publ. 23, 1960:60) includes the Pine Grosbeak (*Pinicola enucleator*) on the hypothetical list since none of the sight records is supported by a specimen. I first observed Pine Grosbeaks on campus November 17, 1960. They were next seen on December 13 and remained in the area until at least February 8, 1961. Groups of two to six were frequently noted, chiefly during snowy periods, in conifers and hackberry trees on or near campus. My series (2 adult females; 2 immature females; 1 immature male) is referable to the race *P. e. leucura*. No adult males were seen. I wish to thank Dr. G. M. Sutton (University of Oklahoma), Dr. R. F. Johnston (University of Kansas), and Mr. R. J. Niedrach and Dr. A. M. Bailey (Colorado Museum of Natural History) for the loan of specimens.—CHARLES A. ELY, *Department of Zoology, Fort Hays Kansas State College, Hays, Kansas, March 14, 1961.*

**Prairie Warbler off the Pacific Coast of Guatemala.**—At 11 a.m. on September 25, 1960, as scattered showers approached from the east, an immature Prairie Warbler (*Dendroica discolor*) flew aboard the freighter, M. S. Oakville, on which I was traveling between Los Angeles and the Panama Canal. We were on a course parallel to and some 190 kilometers southwest of the coast of Guatemala near Tahuesco. At noon, when I last saw the warbler, we were at latitude 12° 37' N and longitude 92° 31' W, about 33 kilometers southeast of our position at 11 a.m.

During the first part of the hour, the warbler hopped about the foredeck and along cables so near me that I almost caught it in my cap. I noted that it wagged its tail in the manner typical of the species as it pecked at tiny objects. Later it perched on the cables amidships, where it was photographed by another passenger, Mr. Harry Grossman of Pomona, California. Mr. Grossman has kindly provided color prints which show clearly the field marks I had noted at close range.

Since this warbler normally winters in Florida and the Caribbean area, this individual was far out of range. The only other record for the Pacific side of Middle America to my knowledge is that of a single bird taken on the Volcán de San Miguel, El Salvador, on March 15, 1926 (Dickey and van Rossem, *Field Mus. Nat. Hist., Zool. Ser. 23, Publ. 406, 1938:1-609*).

Shortly after the rains, several other land birds flew past. That storms bring down migrants aboard ships has been noted several times, particularly for the Gulf of Mexico.—EDWIN WILLIS, *Museum of Vertebrate Zoology, Berkeley, California, March 3, 1961.*

**Turkey Vulture Nesting in Pima County, Arizona.**—While attending the annual meeting of the Cooper Ornithological Society in Tucson, in 1961, some of the local ornithologists remarked that there was no published record of the nesting of the Turkey Vulture (*Cathartes aura*) in the state of Arizona. This leads me to supply two records of sets of two eggs collected by me on Picacho de la Caleria, about 20 miles northwest of Tucson on May 17, 1923, and April 28, 1924. The first nest was near the top of the peak and in a cave under rocks, back about 15 feet from the main entrance. I reached the eggs by lying down and inching my way back five or six feet over trash carried there by pack rats. Fear of rattlesnakes would keep me from going into such a place again. The second set was on bare sand under a large rock high on the hillside.—WILSON C. HANNA, *Colton, California, April 15, 1961.*

**The Amur Barn Swallow off British Columbia.**—On July 15, 1960, while one of us (G.M.C.) was engaged in oceanographic studies from the motor vessel Key West II at a point 90 miles west of Tasu Sound, Queen Charlotte Islands, British Columbia, an adult male swallow came aboard in a weakened condition. It died the following day and was preserved as a specimen for the Museum of Zoology of the University of British Columbia. Dr. H. G. Deignan of the United States National Museum has compared the specimen with series of Asiatic swallows in their collections and determined it as unmistakably of the subspecies *Hirundo rustica gutturalis* Scopoli. This subspecies normally breeds northeastward through Asia as far as Amurland and Japan. There are two previous specimen records from this continent; both were taken on St. Lawrence Island, one in 1934, and the other in 1938 (Friedmann, *Condor*, 41, 1939:37).

This occurrence marks a new southward and eastward record for the race and reflects a rather remarkable overseas crossing, even if the bird came by way of the Aleutian Island chain. Its emaciated condition suggests that it was not a vagrant from the closely adjacent coast of British Columbia.—I. McT. COWAN and GARRY McT. COWAN, *Department of Zoology, University of British Columbia, Vancouver, British Columbia, February 23, 1961.*

## NOTES AND NEWS

The Cooper Ornithological Society is happy to acknowledge the generosity of the David E. Bright Foundation in financing the color plate of Brazilian Manakins appearing in this issue of *The Condor*.

The Society announces the appointment of Dr. Norman R. French of the University of California at Los Angeles as Assistant Business Manager. He assumes Dr. T. R. Howell's duties while the latter spends a year in Central America.

A Committee on Student Participation has been formed, with Professor S. Charles Kendeigh as Chairman, to receive applications from young ornithologists for financial support to enable them to attend the XIII International Ornithological Congress in Ithaca, New York, June 17 to 24, 1962. The funds provided for this Committee are being raised by private donations, and

it is not certain at this time how large a sum will be available. The Committee will presumably be able to make grants only to Graduate Students.

Applications must be submitted to Professor Kendeigh, Vivarium Building, University of Illinois, Wright and Healey Streets, Champaign, Illinois, before April 1, 1962.

Checks of donations for the work of the Committee should be made payable to the American Ornithologists' Union and be mailed to the Treasurer (Professor Charles G. Sibley, Fernow Hall, Cornell University, Ithaca, New York) with instructions that the money is to be used for this purpose.

It is the hope of this Committee that serious young students of ornithology will take advantage of the unique opportunity to attend an International Congress and to meet the world's leading ornithologists in person.—ERNST MAYR, *President, XIII International Ornithological Congress*.

**For Sale, Exchange, and Want Column**—Each member of the Cooper Society is entitled to one short advertising notice in any issue of the Condor free. Notices of over 3 lines will be charged for at the rate of 25 cents per line. Send advertising copy to Jack C. von Bloeker, Jr., Los Angeles City College, 855 N. Vermont Ave., Los Angeles 29, California.

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**FOR EXCHANGE**—Have many *Ornithomyia fringillina* (Diptera: Hippoboscidae) in my possession. Will trade two, any sex, for two, any sex, of other North American Hippoboscidae. Write for details.—GARY C. KUYAVA, 1611 North 7th Ave. East, Duluth 5, Minnesota.

**WANTED URGENTLY**—Vols. I, II, IV, and VI of Peters' "Check-list of Birds of the World," in good condition; please state price.—JAN R. VAN OOSTEN, 301 N. Yakima, Tacoma, Washington.

**FOR SALE**—"Birds of Southern California—An Annotated Field List," by Robert L. Pyle and Arnold Small, 1961 ed., 64 pp. Graphs indicate seasonal status, relative abundance, and preferred localities and habitats of more than 400 species; \$1.15 postpaid.—LOS ANGELES AUDUBON SOCIETY, 7377 Santa Monica Blvd., Los Angeles 46, Calif.

**WANTED**—"Check-list of Birds of the World," Vols. I, II, IV, and VI.—DON BLEITZ, 1001 N. McCadden Place, Los Angeles 38, Calif.

**WANTED**—Pacific Coast Avifauna No. 14, 1921, "The Birds of Montana," by A. A. Saunders.—RICHARD E. JOHNSON, 1534 N. White Ave., Pomona, Calif.

**FOR SALE**—Write for complete specifications and details on Specimen Case no. 112, designed by the University of California. Size 27" × 44" × 42"—priced at \$199.00, F.O.B. Escondido, Calif.—CHAPPELL'S HOUSE OF WOODCRAFT, P. O. Box 1085, Escondido, Calif.

**FOR SALE**—"Birds of the West," by Ernest S. Booth, 1960 edition—an up-to-date field guide for western birds. It contains A.O.U. changes; 413 pages, 280 birds in color, 1000 illustrations; \$5.00 postpaid.—OUTDOOR PICTURES, P. O. Box 1326, Escondido, Calif.

DR. HERBERT FRIEDMANN, Director of the Los Angeles County Museum, states, "Skutch's descriptions of the life histories of Central American birds are a pioneering effort in the same sense that were those of Azara on the birds of Paraguay at the start of the 19th Century. Future generations of ornithologists will look back on *Life Histories of Central American Birds*, by Dr. Skutch as a classic, an original source reference. This monumental work is one of the outstanding ornithological efforts of the 20th Century."

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